

THE BIVALVES OF THE SPILSBY SANDSTONE FORMATION
AND CONTIGUOUS DEPOSITS

by

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To

My Parents

and

to

Derek A. Lee

Abstract.

Hitherto the bivalve fauna of the Spilsby Sandstone and contiguous deposits including the lower part of the Sandringham Sands and Speeton Clay of Middle Volgian to Ryazanian age has been inadequately described. As a consequence of this study 92 taxa have been recorded. 45 of these are described fully and include 13 new species and one new subgenus. Information has been obtained from the author's collecting and from museum collections. Locality and section information is given for sites examined by the author. The preservation of the fauna is normally as moulds, but cold cure silicone rubber has been used to obtain casts with great success.

The ecology of the less well understood bivalves is discussed. Five bivalve dominated assemblages are recognised. They represent various shallow marine facies. The sediments include glauconitic sands and silts with condensed sequences containing phosphatised nodules and also a sideritic ironstone occurs. A facies model is produced for the East Midlands Shelf, and the contemporary relationships with other parts of England are discussed. The Spilsby basin represents a westerly embayment or estuary of the Southern North Sea basin. In Middle Volgian times there were marine connections to the Wessex basin to the south, but with the subsequent draining of this latter area in Upper Volgian to Ryazanian times to restricted marine, brackish and freshwater lagoonal environments, open marine connection ceased. The Spilsby basin remained fully marine during these times, but became more enclosed.

The Spilsby bivalve fauna indicates strong faunal similarities with Boreal regions, and in particular with East Greenland and the Russian Platform. The fauna also compares closely with the sandy Upper Kimmeridgian facies in central England but contrasts strongly with the contemporary faunas of the Portland and Purbeck Beds. The relationships of the Spilsby fauna with other Boreal regions and with Tethyan Europe are discussed.

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Chapter 1. INTRODUCTION.

The Spilsby Sandstone which spans the Jurassic-Cretaceous boundary, occurs in Lincolnshire where it outcrops at the base of the Wolds escarpment. It thins and is cut out to the north in Humberside and to the south merges with the generally finer-grained lower part of the Sandringham Sands around the Wash. The Sandringham Sands in turn thin and are cut out southwards just north of Southey in Norfolk and fragments are found as reworked clasts in the base of the Lower Greensand of Cambridgeshire and Bedfordshire. Pleistocene erratic boulders of Spilsby Sandstone/Sandringham Sands are known as far south as London. The Spilsby Sandstone is predominantly a glauconitic sandstone with calcareous concretions. At its base and near the middle are important phosphate nodule beds. To the south the lower levels of the Sandringham Sands (Roxham and Mintlyn Beds) tend to be more clayey and silty and become a sideritic clay ironstone in the upper part. Phosphatic nodule beds are better developed and more numerous than in the north. At Speeton, in Yorkshire, the basal phosphatic nodule bed of the Speeton Clay is compared with the Basal Spilsby Nodule Bed, while the succeeding clays up to D6 at least are of the age of the upper part of the Spilsby Sandstone. Though not contiguous onshore the Spilsby Sandstone and Speeton Clay are found in contact offshore where the exact age is uncertain. The full stratigraphic and structural settings are discussed in chapter 2.

The bivalve fauna of these strata, subsequently referred to as the Spilsby fauna, has hitherto been poorly described. A limited number of specimens collected last century exist in museum collections. But it was not until Dr. R. Casey began research on the Jurassic-Cretaceous boundary in eastern England during the 1960s that significant collections of well

horizoned bivalves were made. He collected from important exposures in the Sandringham Sands made during the excavations for a flood relief channel and for the North Sea gas pipe-lines in Norfolk. I have made further collections of over 3,000 specimens in the Spilsby Sandstone of Lincolnshire, mostly accurately horizoned according to the stratigraphic scheme of Casey (1973).

The Spilsby bivalve fauna has never been monographed, though some species have been described, especially in Woods' (1899-1912) monograph on the Lower Cretaceous Lamellibranchs. However, in the mid 19th century palaeontologists such as d'Orbigny, Rouillier, Eichwald, Trautschold and others described from the Russian Platform and the Urals, faunas very similar to those described here, and it is to these authors that one turns for the identification of many Spilsby bivalves. During the present century some revision of the older Russian monographs has been attempted (eg. Gerasimov 1955), but unfortunately many of the original collections have been lost or destroyed. Important new faunas have also been described by Zakharov and others during the last decade, principally from Siberia. In recent years the stratigraphic framework of the Jurassic-Cretaceous boundary strata in the USSR based on ammonites (eg. Saks 1972) has provided a much more precise basis for work.

The other area which has had a strong bearing upon the study of the Spilsby fauna is East Greenland. The Mesozoic stratigraphy of the area is only just getting out of the exploration stage (eg. Surlyk, Callomon, Bromley and Birkelund 1973) as the area is still remote and there is no ready access because of the harsh climate. Apart from some early species descriptions, Jurassic and early Cretaceous bivalves have only been

tentatively studied at some horizons (eg. Spath, 1936, 1947) and the stratigraphically important Buchia is in need of serious study.

Acknowledgements.

The work for this thesis was carried out at Queen Mary College (University of London) under the successive Heads of Department, Prof. J. F. Kirkaldy and the late Prof. W. W. Bishop, who kindly made available the facilities of the Department of Geology. Special thanks are due to Dr. P. F. Rawson, my supervisor, for guidance throughout this project.

I am indebted to many people for helpful discussion and for generous access to palaeontological collections and for loan of specimens. They include Dr. R. Casey and Mr. E. Smith (Institute of Geological Sciences, London); Dr. N. Morris and Dr. R. Cleevley (British Museum (Natural History), London); Dr. C.L. Forbes (Sedgwick Museum, Cambridge); Dr. J. W. Neale (University of Hull); Mr. P. Lawrance (Norwich Castle Museum); Miss. A. S. Mottram (King's Lynn Museum); Dr. A. Dhondt (Institut Royale des Sciences Naturelles, Bruxelles); Dr. E. Lanterno (Museum d'Histoire Naturelle, Geneve); Dr. E. Kemper (Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover); Dr. F. Schmid (Niedersächsisches Landesamt für Bodenforschung, Hannover); Dr. T. Birkelund and Dr. R. G. Bromley (Institut for Historisk Geologi og Palaeontologi, Copenhagen); Dr. F. Surlyk (Mineralogisk Museum, Copenhagen); Dr. K. Kleeman (Zoological Institute, Vienna); Dr. J. A. Jeletzky (Geological Survey of Canada, Ottawa); Dr. E. Kauffman (National Museum of Natural History, Washington).

Chapter 2. STRATIGRAPHY.

Introduction.

The recent phase of hydrocarbon exploration in the North Sea has demanded a full structural and sedimentary understanding of the area and the adjacent land. First the structural setting is examined from a general point of view. Further structural information is discussed together with the stratigraphy of each sedimentary basin in turn. Nomenclature especially for the structural features is still in a state of flux, but nomenclature here follows Rawson et al. (1977 in press).

Structural Setting.

The area under consideration (fig. 2.1) stretches from Yorkshire to Bedfordshire and comprises the western end of the Southern North Sea Basin. Part is termed the East Midland Shelf (Kent, 1975) which is bounded to the north by the Market Weighton Hinge and to the east by the Dowsing Fault with the Sole Pit Trough immediately to the north east. To the south and south east lies the London Brabant Massif and to the west the Pennine Anticline (See also Rhys 1974, fig. 8). North of the Market Weighton Hinge lies the Yorkshire basin which in turn is bounded to the north by the Mid North Sea High. The westerly extension of the Spilsby Sandstone and associated strata is conjectural; however beyond the present outcrop pattern, there appears to have been some marine connection across the south Midlands to the Wessex basin at least during part of the Middle Volgian. To the east there was open connection with the rest of the southern North Sea Basin.

With reference to the Spilsby Sandstone and associated strata

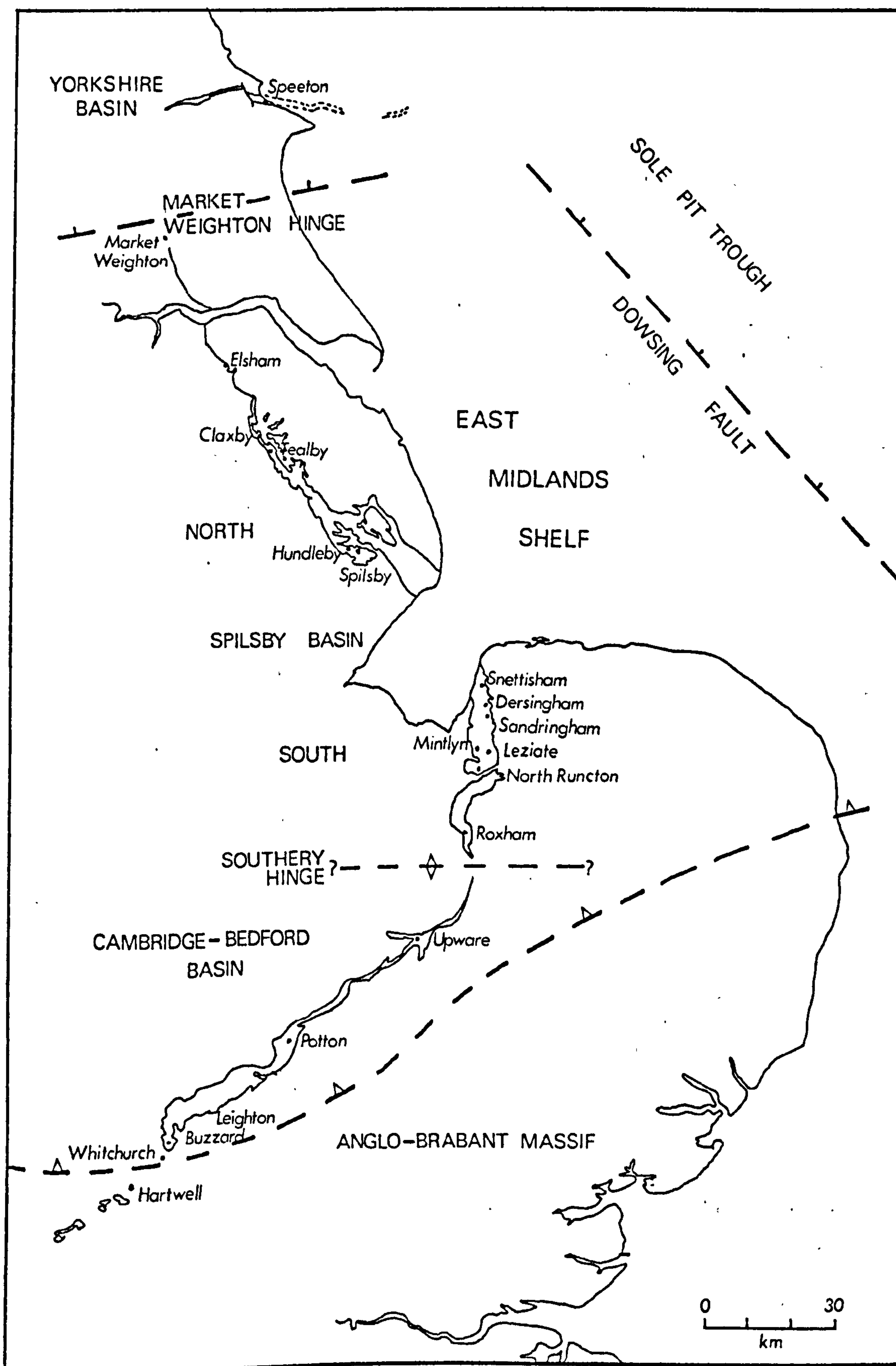


Fig. 2.1.

Outcrop of Lower Cretaceous strata in eastern England, including the basal parts of the Spilsby and Sandringham Formations, but excluding the Gault and Red Chalk. The structural features are shown together with principal localities of stratigraphic significance.

the East Midlands Shelf and Yorkshire basin are best illustrated in strike section from north to south as shown partly on Fig. 2.2. The basins are as follows and are described from north to south:

	Yorkshire Basin
East Midlands	{ Spilsby Basin
Shelf	
	{ Cambridgeshire-Bedfordshire Basin

The stratigraphical sequence used here is that of Casey (1973), and is summarised in Figure 2.3.

Yorkshire Basin

The most northerly basin is the Yorkshire Basin (Arkell 1933, Speeton basin of Casey 1963). Onshore only the southern outcrop of the Lower Cretaceous part is seen at Speeton and for 10 km. inland. The Speeton Clay as a whole is about 100 m thick at Speeton and 365 m inland at Fordon (Dilley in discussion of Neale 1968) although only between 4 and 6 m at the base are contemporary with the Spilsby Sandstone. The thickening of the Speeton Clay inland could be attributed to contemporary movement of the Hunmanby Fault. The outcrop is traceable offshore for about 40 km (Dingle 1971) and disappears under the Chalk. The offshore situation is summarised by Pegrum, Rees and Naylor (1975, p.86, fig. 16). The Yorkshire basin appears to have been the landward extension of the Sole Pit Trough. South of the onshore outcrop the Speeton Clay thins rapidly to zero towards the Market Weighton Structure. Jeans (1973) favours Versey's (1929) suggestion that the northern margin of this structure is a continuing contortion zone of the Gilling Fault which probably controlled Lower Cretaceous sedimentation. The possibility that

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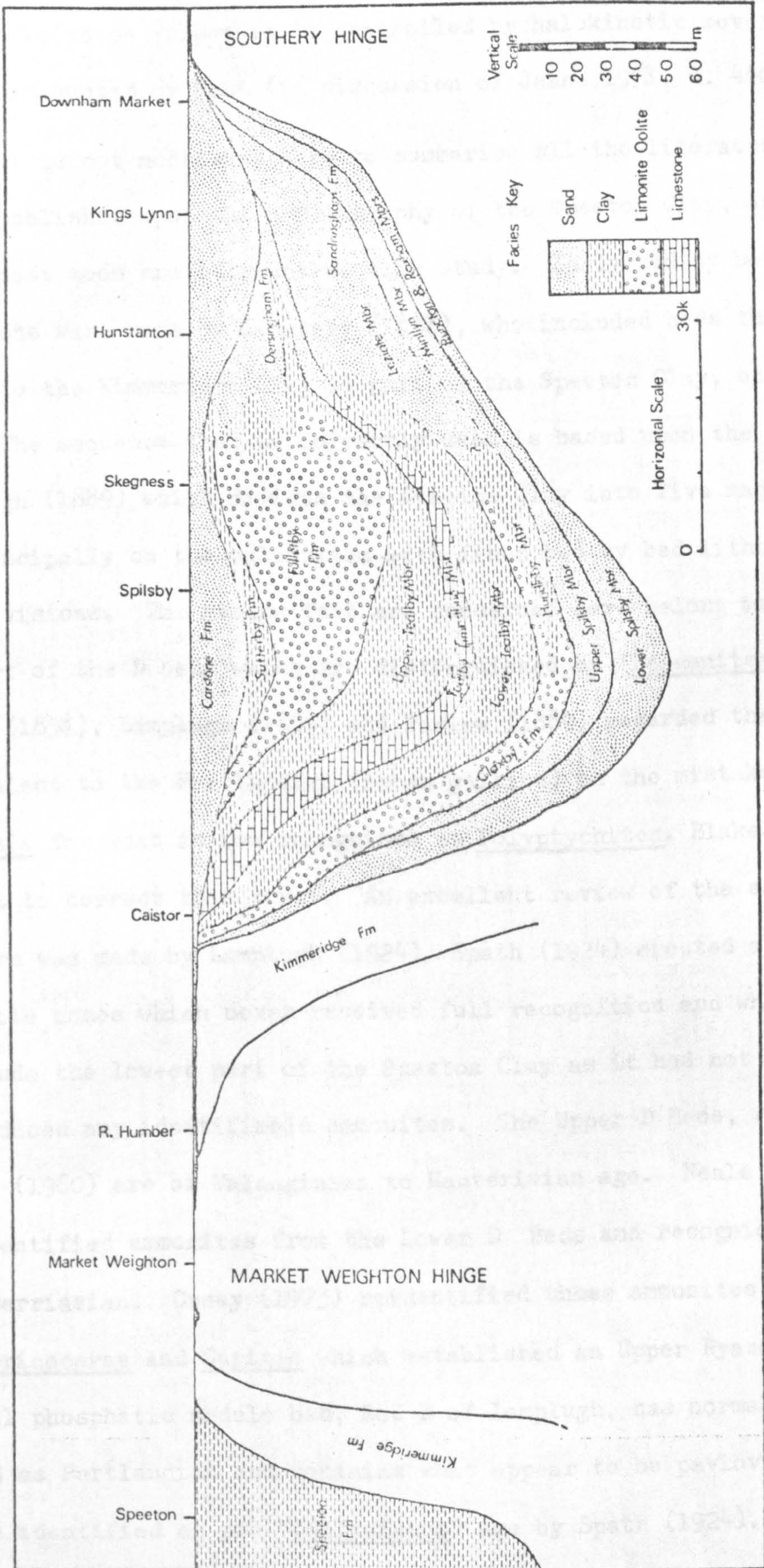


Fig.2.2 Generalised facies reconstruction along strike from Yorkshire to Norfolk in late Jurassic and Lower Cretaceous times.

the Market Weighton Structure is controlled by halokinetic movements has been discounted by Kent (in discussion of Jeans 1973, p. 440).

It is not necessary here to summarise all the literature that has been published upon the stratigraphy of the Speeton Clay, as only the lowermost beds are relevant to this study. Early bed by bed descriptions were made by Leckenby (1858), who included beds that belonged to the Kimmeridge Clay as part of the Speeton Clay, and Judd (1868). The sequence that is currently used is based upon the description by Lamplugh (1889) which divides the Speeton Clay into five major units based principally on the belemnites with finer bed by bed lithological/faunal divisions. The strata that are concerned here belong to the lower part of the D beds which are distinguished by 'Belemnites lateralis'. Leckenby (1858), Lamplugh (1889) and Pavlow (1889) regarded the D beds as equivalent to the Portlandian (*sensu gallico*) on the mistaken identity as Gravesia for what is now recognised as Polyptychites. Blake (1891) was the first to correct this error. An excellent review of the earlier literature was made by Lamplugh (1924). Spath (1924) erected a sequence of ammonite zones which never received full recognition and which did not include the lowest part of the Speeton Clay as it had not at this time produced any identifiable ammonites. The Upper D Beds, redescribed by Neale (1960) are of Valanginian to Hauterivian age. Neale (1962) first identified ammonites from the Lower D Beds and recognised their age as Berriasian. Casey (1973) reidentified these ammonites principally as Peregrinoceras and Surites which established an Upper Ryazanian age. The basal phosphatic nodule bed, Bed E of Lamplugh, has normally been regarded as Portlandian and contains what appear to be pavloviid ammonites although identified as pre "pallasianus" age by Spath (1924). However

Yorks. Basin		N Spilsby Basin		S	Zone	Stage
Speeton Formation	? ?	Hundleby Mbr	Sandringham Formation	Leziate Mbr (pars)	<u>Paratollia</u>	Valanginian (pars)
	D6A	Claxby Fm			<u>Peregrinoceras albidum</u>	Upper Ryazanian
	D7E	Ferruginous Grit			<u>Surites (Bojarkia) stenomphalus</u>	
	D7F					
	? ?	Upper Spilsby Mbr		Mintlyn Mbr	<u>Surites (Lynnina) icenii</u>	
	D8	Mid Spilsby Nodule Bed			<u>Hectoroceras kochi</u>	Lower Ryazanian
					<u>Runctonia runctoni</u>	
					<u>Subcraspedites (Volgidiscus) lamplughii</u>	Upper Volgian
				Runcton Mbr	<u>Subcraspedites (Subcraspedites) preplicomphalus</u>	
					<u>Subcraspedites (Swinertonia) primitivus</u>	
		Lower Spilsby Mbr			<u>Paracraspedites oppressus</u>	Middle Volgian (pars)
		Basement Beds				
	Coprolite Bed E	Basal Spilsby Nodule Bed		Roxham Mbr	<u>Titanites giganteus</u>	
Kimmeridge Fm	F	Kimmeridge Fm	Kimmeridge Fm		<u>Pectinatites</u> spp.	Lower Volgian (pars)

Fig. 2.3

Middle Volgian to Upper Ryazanian stratigraphic scheme for the Yorkshire and Spilsby Basins.

the lowest D beds have not yet produced ammonites. The belemnite Acroteuthis lateralis has been recorded occurring immediately above the Coprolite bed in D8, as one of the zonal indices of Lamplugh (1889). Its age has been regarded as lowest Cretaceous and this is confirmed by the work of Pinckney and Rawson (1974). In further discussions of the Speeton section, the lithological subdivisions of Neale (1962) are followed.

The Spilsby Basin.

Although originally termed the Lincolnshire - Norfolk Province by Casey (1961a, p.503) the subsequent term Spilsby Basin (Casey 1963, p.2) appears to be more firmly entrenched in the literature. The Spilsby Sandstone and Sandringham Sands outcrop runs from just north of Caistor in Humberside to south of Roxham in Norfolk. The basin is asymmetrical as shown in Fig. 2.2, and is thickest at the southern end of the Lincolnshire Wolds where the Spilsby Sandstone is about 30m. thick. To the north the basin is bounded by the Market Weighton structure and to the south by the Southery Hinge, which is introduced as a term for the provincial boundary marked by Casey (1961a p.503) and which is also a distinct structural feature. Both the Market Weighton and Southery structures appear to have been positive in the late Jurassic and Lower Cretaceous. Jeans (1973) has postulated that a fault could exist on the southern margin of the Market Weighton structure but this was not accepted by Rawson (in discussion, p.441) who preferred to regard it as a tilted margin dipping into the seas of the Spilsby Basin. The Southery Hinge probably remained submergent through Jurassic Cretaceous boundary times.

The north part of the Spilsby Basin contains the Spilsby Sandstone. Early workers described the sandstone but did not name it. Bogg (1816)

described the succession in the Lincolnshire Wolds and Dikes and Lee (1837) described the geology of Nettleton Hill. Judd (1867) used the term Lower Sand and Sandstone, while Strahan (1886) first introduced the term Spilsby Sandstone. Swinnerton (1935) proposed a tripartite division of the sandstone. (The stratigraphic schemes of these earlier workers are summarised in Figure 2.4.) Casey (1963) proposed a bipartite division (see Fig. 2.3): the Lower Spilsby Sandstone incorporates the Basement Beds and the lower part of the glauconitic sands of Swinnerton and the Upper Spilsby Sandstone with the Mid Spilsby Nodule bed at its base includes the upper part of the Glauconitic Sands and the Ferruginous Grit.

Generally regarded as being of Neocomian age, the Spilsby Sandstone was first recognised as spanning the Jurassic-Cretaceous boundary by Pavlow (1889). The belemnite zonation of Lamplugh (1889) placed the Spilsby Sandstone within the B. lateralis Zone, of basal Cretaceous age. But true lateralis has only been found in the Upper Spilsby Sandstone (Pinckney and Rawson 1974). Spath (1924) recognised three 'Infravalanginian' ammonite zones in the Spilsby Sandstone believing it to be entirely Cretaceous and this idea was followed by Swinnerton (1935) who described species of Paracraspedites and Subcraspedites from the Basement beds. Even Arkell (1933) accepted the Cretaceous age. However Casey (1962) first suggested that Paracraspedites and Subcraspedites were late Jurassic ammonites and in 1964 he recorded Paracraspedites from the Portland Beds of Dorset. Finally (Casey 1973) full lithostratigraphical and biostratigraphical information was published for the Spilsby Sandstone (see Fig. 2.3) and the age was shown to extend from the Middle Volgian into the late Ryazanian. This scheme is followed here.

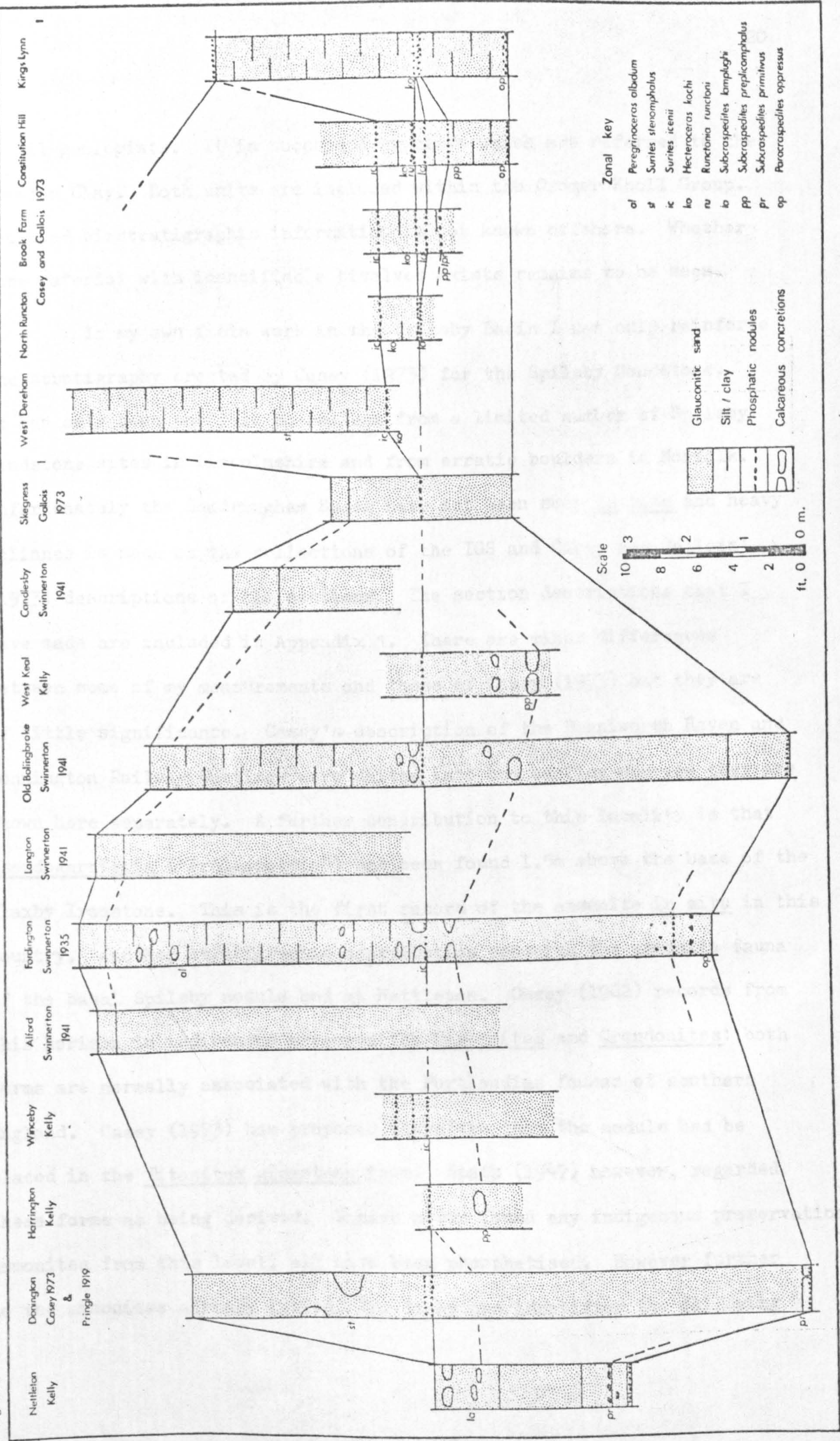
Bogg 1816	Dikes & Lee 1837	Judd 1867	Strahan 1886	Swinerton 1935		
Chalk	Red Chalk	Hunstanton Red Rock	Red Chalk			Red Chalk
Coarse brown pebbly sand	Thoresway Sand	Upper Ferruginous Sands	Carstone	Langton Series		Carstone Grit
						Carstone Sand and Clay
						Sutterby Marl
Oolite	Grey Stone	Tealby Series	Upper Ironstone and Clay	Tealby Series	Fulletby Beds	Upper Roach
						Roach Stone
			Lower Roach			
			Tealby Limestone		Tealby Beds	Upper Tealby Clay
						Tealby Limestone
	Tealby Clay	Lower Tealby Clay				
	Greensand and Sandstone	Lower Sand and Sandstone	Lower or Claxby Ironstone	Claxby Beds	Upper Ironstone	
					Hundleby Clay	
					Lower Ironstone	
			Spilsby Sandstone		Spilsby Beds	Ferruginous Grit
Glauconitic Sands						
Basement Beds						
Grains of quartz				Spilsby Series	Kimmeridge Clay	
Shale stratum	Kimmeridge Clay	Blue Clay and Slatey beds	Oolite	Kimmeridge Clay		

Fig. 2.4 Table of early stratigraphic schemes for the strata below the Chalk of the Lincolnshire Wolds.

The south part of the Spilsby basin is occupied by the Sandringham Sands and some later deposits in Norfolk, of which only the lower parts are equivalent to the Spilsby Sandstone and are discussed below. Until recently the very poor state of exposure in Norfolk made lithological division of the Sandringham Sands difficult as localities were scarce. Rose (1835, 1862) referred these sands to the Lower Greensand but Whitaker and Jukes-Browne (1899) introduced the name Sandringham Sands. The first definite indication of a precise early Cretaceous age for these beds was given by Casey (1961b) when he recorded Hectoroceras from the West Dereham Flood Relief Channel. The age was believed to be Berriasian as the genus had been described previously only from East Greenland. With further information made available by the North Sea gas pipelines, Casey and Gallois (1973) established a detailed lithostratigraphy for the sands and divided the lower part into the Mintlyn, Roxham and Runcton beds and that the ammonite sequence is fuller than in Lincolnshire (see Fig. 2.4, adapted from Casey 1973). Further support for the age of these strata comes from Ager (1971) who compared Spilsby Sandstone brachiopods from erratic boulders in East Anglia with Middle and Upper Volgian forms from the Russian Platform, and Creber (1972) who recognised Upper Jurassic Gymnospermiferous wood in the Roxham Beds. Supplementary published stratigraphic information about the location of the basal and mid Spilsby nodule bed in the Spilsby Sandstone and Sandringham Sands is contained in the reports of Gallois (1973) and Gallois and Cox (1974). These reports are concerned primarily with the correlation of the topmost Kimmeridge Clay.

Offshore (Rhys, 1974) on the East Midlands Shelf, the Spilsby Sandstone is recognised as a distinctive 'basal Cretaceous' sandstone

Fig. 2.5. Correlation of the principal sections of Spilsby and Sandringham Formations from Humberside to Norfolk.



by oil geologists. It is succeeded by clays which are referred to the Speeton Clay. Both units are included within the Cromer Knoll Group. Detailed biostratigraphic information is not known offshore. Whether core material with identifiable bivalves exists remains to be seen.

In my own field work in the Spilsby Basin I can only reinforce the stratigraphy erected by Casey (1973) for the Spilsby Sandstone. It has only been possible to collect from a limited number of Spilsby Sandstone sites in Lincolnshire and from erratic boulders in Norfolk. Unfortunately the Sandringham Sands have not been seen in situ and heavy reliance is made on the collections of the IGS and Casey and Gallois' (1973) descriptions of the sections. The section descriptions that I have made are included in Appendix 1. There are minor differences between some of my measurements and those of Casey (1973) but they are of little significance. Casey's description of the Benniworth Haven and Donnington Railway Cuttings were united into one section whereas they are shown here separately. A further contribution to this locality is that Pseudogarnieria ("Proleopoldia") has been found 1.5m above the base of the Claxby Ironstone. This is the first record of the ammonite in situ in this country. Another stratigraphic contribution concerns the ammonite fauna of the basal Spilsby nodule bed at Nettleton. Casey (1962) records from this horizon in indigenous preservation Kerberites and Crendonites: both forms are normally associated with the Portlandian faunas of southern England. Casey (1973) has proposed therefore that the nodule bed be placed in the Titanites giganteus zone. Spath (1947) however, regarded these forms as being derived. I have never found any indigenous preservation ammonites from this level, all have been phosphatised. However further to the ammonites already listed, Dr. Casey has identified the following

typical Middle Volgian genera from my collections:-

Epilaugeites, Lomonosovella and Pavlovia, all in phosphatised condition.

A summary of the principal sections in the Spilsby Sandstone and lower part of the Sandringham Sands is shown in Figure 5. The distribution of zonal ammonites where known is marked.

In post Ryazanian times the margins of the Spilsby Basin were eroded and reworked Spilsby Sandstone and associated deposits appear as clasts in later strata. In the north the Spilsby Sandstone is progressively cut out under the base of the Claxby Ironstone. The Upper Spilsby Sandstone only reaches as far north as about Tealby, where the mid Spilsby nodule bed is cut out. At Nettleton, the S. lamplughii Zone rests immediately under the Claxby Ironstone, the basal unit of which sharply overlies the underlying sandstone and contains a rich and varied bivalve fauna some of which may be reworked from the Spilsby Sandstone. North of Caistor the Spilsby Sandstone thins rapidly and is finally cut out by the Carstone which has overstepped all the other units of Lower Cretaceous age. Rolled phosphatised bivalves and ammonites of the Spilsby Sandstone have been found by Dr. P.F. Rawson in the base of the Carstone at Nettleton. Furthermore a supposedly synclinal relic of Spilsby Sandstone at Elsham (eg. Wilson, 1948, fig. 18) is of Lower Kimmeridgian age (Kent and Casey, 1963). To the south, Casey and Gallois (1973) discuss the occurrence of reworked Sandringham Sands and their Lower Cretaceous fauna in the base of the Carstone in south Norfolk.

Pleistocene erosion of the Spilsby Sandstone/Sandringham Sands has caused much of East Anglia to be littered with tough calcareous concretions. The distribution of these erratics is plotted in Figure 2.6,

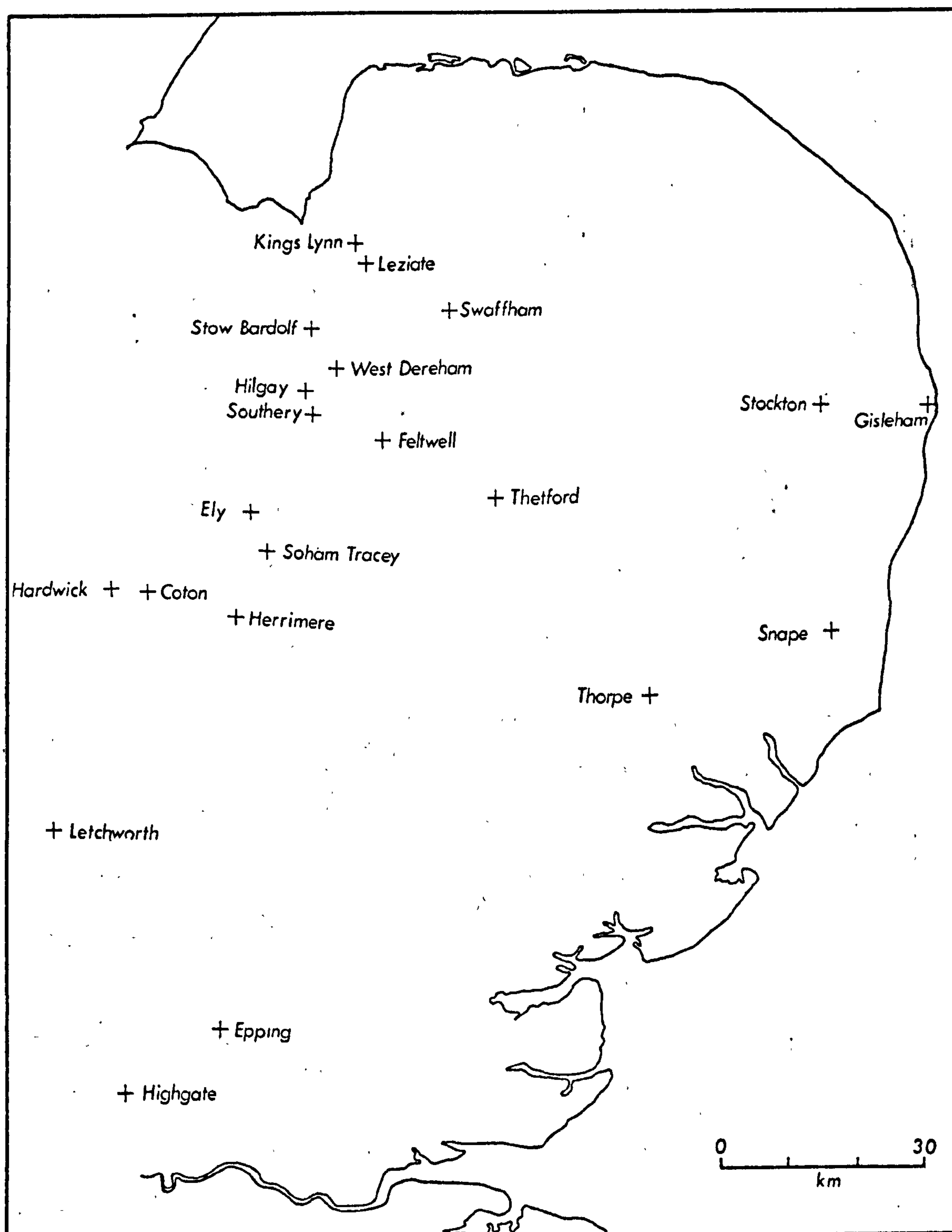


Fig. 2.6.

Distribution in East Anglia of erratic blocks of Spilsby Sandstone/Sandringham Sands. The data from which the figure is compiled is listed in Appendix 2.

which has been compiled from various published sources listed in Appendix 2. The concentration of the erratics appears to be greatest in southwest Norfolk and thins southwards and eastwards through East Anglia as far south as London. Casey (1973, p. 208) suggests that the origin of these boulders is in the offshore region of southern Lincolnshire. The extensive cover of Chalk on the sea bed here restricts the area to the close inshore region of the Wash. It is also possible that these erratics came from the onshore area of the southern Lincolnshire Wolds as the matrix of some of the boulders can be closely tied in with horizons in measured sections in the area, or with comparable horizons in the lower part of the Sandringham Sands. Ammonite faunas of the following zones have been recognised:

T. giganteus, R. oppressus, S. preplicomphalus and P. albidum.

The Cambridge Bedford Basin.

Although originally termed the Cambridge Bedford Province by Casey (1961a, p. 503), the name is modified to basin. Casey (1963) p. 2 was inclined to place this within the Spilsby Basin but it is retained here as a separate entity until further information is available. Clasts of Spilsby/Sandringham type sediments occur in the base of the Lower Greensand indicating the existence of former Jurassic-Cretaceous boundary sediments in the area, but whether they were originally deposited in a discrete basin is arguable. The outcrop pattern of the Lower Greensand shows a distinct syncline, but this could have been controlled either by post or contemporaneous Aptian movements. The southern boundary of the basin may not have existed in Jurassic Cretaceous boundary times in the area of the Midlands high. The basin was marginal to the London Landmass to the east, but to the west beyond the outcrop pattern the

margins are speculative.

The early descriptions of the geology of the Cambridge-Bedford basin are summarised in Teall (1875) who provided a detailed discussion and faunal list from the 'Potton and Wicken Phosphatic Deposits.' Keeping (1883) discussed the strata in more detail and described many species. Both these authors recognised an indigenous fauna that compared largely with the Aptian of southern England. They also recognised important derived faunas preserved principally as reworked phosphatised moulds together with saurian bones representing strata from Oxfordian to Neocomian in age. Keeping recognised a 'dark grit' type of phosphatised nodule and from it lists an extensive fauna part of which he compared to the 'Donnington Sands' fauna of Lincolnshire and to that in the derived blocks of sandstone in East Anglia, i.e. Spilsby Sandstone. Casey (1961a) recognised the indigenous deposits as Lower Greensand of Upper Aptian age, while Lower Aptian material was present as part of the derived fauna. He also noted that the basal conglomerate at Ridgmont in Hertfordshire contained reworked elements of the Hartwell Clay. Middlemiss (1962a, 259-260) reviewed the derived fauna of this basin and (1962b, p. 618) discussed affinities with the basal Spilsby Nodule bed on the presence of brachiopods.

Chapter 3. PALEONTOLOGY OF THE BIVALVES.

Introduction.

The bivalves of the Spilsby Sandstone and contemporary deposits in eastern England have received only occasional attention in the past. J. de C. Sowerby (1827) described Lucina crassa from Horncastle. Lycett (1872) described Trigonia ingens from the presumed drift of Norfolk and T. tealbyensis from Lincolnshire. Some of the fauna described by Keeping (1883) represents reworked Spilsby species - Cucullaea vagans and C. donningtonensis. Pavlow (1896) figured Aucella volgensis (Lahusen) and described a new subspecies var. radiolata. Woods (1899-1912) also described Astarte claxbiensis, Lucina sp., Panopea spilsbiensis and Pleuromya orbigniana, all from the Spilsby Sandstone of Lincolnshire. Finally Casey (1952) described Procyprina centralis from the Spilsby Sandstone. In addition to these formal descriptions and illustrations, there are several published faunal lists principally in the reports of the Geological Survey. They are summarised in Appendix 3. The names are often inaccurate and uninterpretable. There is an important collection (Thurrell 1957 unpublished) from the top of the Spilsby Sandstone at Biscathorpe where Peregrinoceras albidum was recorded by Casey (1973). It has not been possible to include the particularly well preserved bivalves of this collection in this study, but it is intended to examine them fully with Dr. Casey shortly.

So far I have recognised 92 taxa, including 13 new species and one new subgenus in the Spilsby Sandstone, the lower part of the Sandringham Sands and in beds D5-D8 of the Speeton Clay. They are tabulated below. There is inadequate space in this thesis to describe the whole fauna and it is therefore necessary to restrict the descriptions to those bivalve

taxa that are of greatest significance and those that represent new species. The taxa marked (*) below are described herein. A summary of the stratigraphic distribution of the Spilsby Bivalves is shown in Figure 3.1, while the faunal lists based on bed by bed collecting are given in Appendix 1.

Nuculoma variabilis (J. de C. Sowerby)

Barbatia cf. mysis (de Loriol)

*Grammatodon (Grammatodon) schourovskii (Rouillier & Vossinsky)

* " " spilsbiensis sp. nov.

* " (Cosmetodon) compressiusculum (Rouillier & Vossinsky)

* " " productum (Rouillier & Vossinsky)

*Cucullaea (Dicranodonta) vagans Keeping

* " " benniworthensis sp. nov.

*Musculus (Musculus) fischerianus (d'Orbigny)

* " " derehamensis sp. nov.

" " sp.

Lithophaga sp.

Modiolus (Modiolus) sibiricus (Bodylevsky)

Modiolus (Modiolus) aff. vicinalis (Eichwald)

Falciomytilus suprajurensis Cox

Pinna (Pinna) suprajurensis D'Orbigny

" " cf. constantini de Loriol

" " aff. subcuneata Eichwald.

Stegoconcha sp.

Inoceramus cf. pseudoretrorsus (Gerasimov)

*Anopaea brachowi (Rouillier)

* " sphenoidea Gerasimov

Isognomon aff. cuneatum Zakharov

Mulletia sp.

Oxytoma (Oxytoma) octavia (d'Orbigny)

*Arctotis intermedia Bodylevsky

*Entolium (Entolium) orbiculare (J. Sowerby)

*Camptonectes (Camptonectes) morini (de Lorient)

* " (Boreionectes) cinctus (J. Sowerby)

* " (Camptochlamys) cf. intertextus (Roemer)

*Buchia rugosa (Fischer de Waldheim)

*Buchia volgensis (Lahusen)

Plicatula (Plicatula) producta (Rouillier & Vossinsky)

Placunopsis distracta (Eichwald)

Pseudolimea arctica Zakharov

Limea bodylevskii Zakharov

. Plagiostoma planicosta (Trautschold)

" subrigida (Roemer)

" sp.

Liostrea plastica (Trautschold)

" ? gigantea (J. Sowerby)

Nanogyra thurmanni (Etallon)

*Iotrigonia atlantica sp. nov.

*Laevitrigonia (Laevitrigonia) manseli (Lycett)

* " " wightensis (Strand)

*Myophorella (Myophorella) intermedia (Fahrenkohl)

* " " keepingi (Lycett)

* " " tealbyensis (Lycett)

* " " claxbiensis sp. nov.

*Codakia? cf. crassa (J. de C. Sowerby)

*Mesomiltha? cf. kostromensis (Gerasimov)

*Discoloripes fischerianus (d'Orbigny)

* " cf. inaequalis (d'Orbigny)

* " septentrionalis sp. nov.

Myoconcha (Myonconcha) cf. portlandica Blake

*Neocrassina (Lyabinella) asiatica (Zakharov)

* " " laevis (Woods)

* " " groenlandica sp. nov.

* " (Pressastarte) pelops (d'Orbigny)

* " " woldsi sp. nov.

Nicaniella (Nicaniella) mnewnikensis (Milaschwitch)

* " (Trautscholdia) claxbiensis (Woods)

Protocardia (Protocardia) concinna (von Buch)

?Protocardia sp.

Senis aff. petschorae (Keyserling)

Tellinidae indet.

Sowerbya longior Blake

Tancredia sp.

Corbicellopsis claxbiensis (Woods)

*Anisocardia (Antiquicyprina) lincolnshirensis sp. nov

* " " sandringhamensis sp. nov.

Hartwellia (Hartwellia) hartwellensis (J. Sowerby)

* " " mintlyni sp. nov.

* " (Claxbya) cancriniana (d'Orbigny) subgen. nov.

Procyprina centralis Casey

Corbula sp.

*Gastrochaena sp.

*Hiatella (Pseudosaxicava) foetida (Cox)

Martesia constricta Phillips

Pholadomya (Pholadomya) interrupta Eichwald

" " mediana Eichwald

" " aff. speetonensis Woods

*Girardotia compressa (J. de C. Sowerby)

* " wrighti sp. nov.

*Goniomya (Goniomya) rawsoni sp. nov.

Gresslya sp.

Pleuromya orbigniana (Rouillier & Vossinsky)

" spilsbiensis (Woods)

" cf. uniformis (J. Sowerby)

Thracia depressa (J. Sowerby)

" phillipsi (Roemer)

Preservation.

In the Spilsby Sandstone and Sandringham Sands bivalves are usually found as moulds in the concretionary horizons, either in calcareous cemented sandstone or phosphatised nodules. In unconsolidated sands and silts they are not normally preserved. Silicone rubber casting techniques have been used to obtain casts of the shells with great success (See preparation techniques, Appendix 4). Calcitic shells are sometimes preserved in the cores of large calcareous concretions. Aragonite itself is rare if not absent in these formations. Some moulds within calcareous concretions are secondarily filled with sparry calcite, while some mould infillings in the phosphate nodule horizons, although with apparent nacreous shell are completely replaced by phosphorite. Composite moulds are found in the less

indurated horizons. In the Speeton Clay, both calcitic and aragonitic shell is preserved although frequently crushed.

Location of Specimens.

Abbreviations for the principal collections which have been consulted in the preparation of this work are as follows:-

BMNH	British Museum (Natural History), London.
GSC	Geological Survey of Canada, Ottawa.
IGS	Institute of Geological Sciences, London.
IHGPC	Institute of Historical Geology and Palaeontology, Copenhagen.
LM	King's Lynn Museum, Norfolk.
NCM	Norwich Castle Museum.
NLfB	Niedersächsisches Landesamt für Bodenforschung.
NMNH	National Museum of Natural History, Washington.
OUM	Oxford University Museum.
PFR	P.F. Rawson Collection.
SMC	Sedgwick Museum Cambridge.
SRAK	S.R.A. Kelly Collection.

Systematic Palaeontology.

The bivalve classification of Newell in the 'Treatise' (Moore Ed. 1968) is followed here. Generic diagnoses are only given when information is available additional to that in the Treatise.

Richter (1948) introduced a system of annotating synonymy lists to indicate the degree of confidence in allocation of each entry. The

Stage		MIDDLE VOLGIAN		UPPER VOLGIAN			RYAZANIAN				
Zone		Titanites giganteus	Paracraspedites oppressus	Subcraspedites primitivus	Subcraspedites preplicomphalus	Subcraspedites lamplughi	Runctonia runctoni	Hectoroceras kochi	Surites icenii	Surites stenomphalus	Peregrinoceras albidum
Taxa											
<u>Barbatia cf. mysis</u>											
<u>Grammatodon schourovskii</u>			-?-								
<u>Grammatodon productum</u>											
<u>Grammatodon comoressiusculum</u>											
<u>Cucullaea vagans</u>		-?-									
<u>Modiolus vicinalis</u>											
<u>Pinna constantini</u>											
<u>Oxytoma octavia</u>											
<u>Entolium orbiculare</u>											
<u>Camptonectes morini</u>											
<u>Camptonectes cf. intertextus</u>											
<u>Buchia rugosus</u>											
<u>Plicatula producta</u>											
<u>Placunopsis distracta</u>										-?-	
<u>Pseudolimea arctica</u>											
<u>Plagiostoma planicosta</u>											
<u>Plagiostoma sp.</u>											
<u>Liostrea plastica</u>											
<u>Nanogyra thurmanni</u>											
<u>Discoloripes aff. inequalis</u>											
<u>Neocrassina asiatica</u>		-?-									
<u>Neocrassina pelops</u>											
<u>Nicaniella mnewnikensis</u>								-?-			
<u>Nicaniella claxbiensis</u>											
<u>Anisocardia lincolnshirensis</u>											
<u>Hartwellia hartwellensis</u>											
<u>Hartwellia cancriniana</u>											
<u>Gastrochaena sp.</u>											
<u>Hiatella foetida</u>											
<u>Pholadomya interrupta</u>											
<u>Pholadomya aff. speetonensis</u>											
<u>Girardotia compressa</u>											
<u>Gresslya cf. alduini</u>											
<u>Pleuromya uniformis</u>											
<u>Thracia depressa</u>							-?-				
<u>Musculus fischerianus</u>											
<u>Modiolus sibiricus</u>											
<u>Falcimyltilus suprajurensis</u>											
<u>Isognomon cuneatum</u>											
<u>Arctotis intermedia</u>											
<u>Iotrigonia atlantica</u>			-?-	-?-							
<u>Myophorella intermedia</u>											
<u>Codakia? crassa</u>											
<u>Mesomiltha? kostromensis</u>											
<u>Neocrassina woldsi</u>											
<u>Senis aff. petschorae</u>											

Taxa \ Zone	Zone									
	Titanites giganteus	Paracraspedites oppressus	Subcraspedites primitivus	Subcraspedites preplicomphalus	Subcraspedites lamplughii	Runtonia runtoni	Hectoroceras kochi	Surites icenii	Surites stenomphalus	Peregrinoceras albidum
<u>Anisocardia sandringhamensis</u>										
<u>Pleuromya spilsbiensis</u>		-?-								
<u>Plagiostoma subrigida</u>										
<u>Goniomya rawsoni</u>							-?-			
<u>Myophorella tealbiensis</u>										
<u>Grammatodon spilsbiensis</u>										
<u>Pinna aff. subcuneata</u>								-?-		
<u>Anopaea sphenoidea</u>										
<u>Discoloripes fischerianus</u>										
<u>Protocardia concinna</u>										-?-
<u>Sowerbya longior</u>										
<u>Corbicellopsis claxbiensis</u>										
<u>Procyprina centralis</u>										
<u>Corbula sp.</u>										
<u>Anopaea brachowi</u>										
<u>Mulletia sp.</u>					-?-	-?-				
<u>Camptonectes cinctus</u>										
<u>Discoloripes septentrionalis</u>									-?-	
<u>Myoconcha cf. portlandica</u>										
<u>Tancredia sp.</u>										
<u>Martesia constricta</u>									-?-	
<u>Neocrassina groenlandica</u>						-?-				
<u>Nucula variabilis</u>										
<u>Myophorella keepingi</u>										
<u>Tellinidae indet.</u>										
<u>Hartwellia mintlyni</u>										
<u>Pholadomya mediana</u>										
<u>Girardotia wrighti</u>										
<u>Thracia phillipsi</u>										
<u>Liostrea gigantea</u>								-?-		
<u>Buchia volgensis</u>									-?-	
<u>'Protocardia' sp.</u>										
<u>Barbatia sp.</u>										
<u>Cucullaea benniworthensis</u>										
<u>Musculus sp.</u>										
<u>Stegoconcha sp.</u>										
<u>Limea bodylevskii</u>										
<u>Myophorella claxbiensis</u>										
<u>Neocrassina laevis</u>										

Figure 3.1 .

Stratigraphic distribution of the bivalves of the Middle Volgian to Ryazanian of Eastern England. Key:

----- observed occurrence
 -?- possible occurrence
 - - - inferred occurrence

symbols used here follow the usage of Matthews (1973) and are listed below:

- *1900 The species is valid from this date
- .1901 The author is satisfied that the cited synonym is the same species.
- v1902 The author has seen the cited specimen.
- p1903 Part of the cited reference belongs in synonymy
- ?1904 The reference is questionably referred to the species
- 1905 The reference does not add new systematic information
- non1906 The reference is not a synonym.
- 1907 It is not possible to qualify the reference.

Several symbols may be used together where appropriate.

Specific diagnoses are given for most taxa, including ones which do not represent new species. They are designed to aid rapid identification of forms without the user having to extract diagnostic information from the full description of the specimens.

The terms large, medium and small refer to the maximum shell dimension, usually length, and are >60 ; <60 and >20 ; and <20 mm respectively. Measurements given with descriptions are of figured specimens (see plates). The symbols used for the measurements are explained in text figures.

Class	BIVALVIA Linné, 1758
Subclass	PTERIOMORPHIA Beurlen, 1944
Order	ARCOIDA Stoliczka, 1871
Superfamily	ARCACEA Lamarck, 1809
Family	PARALLELODONTIDAE, Dall, 1898
Subfamily	GRAMMATODONTINAE Branson, 1942.

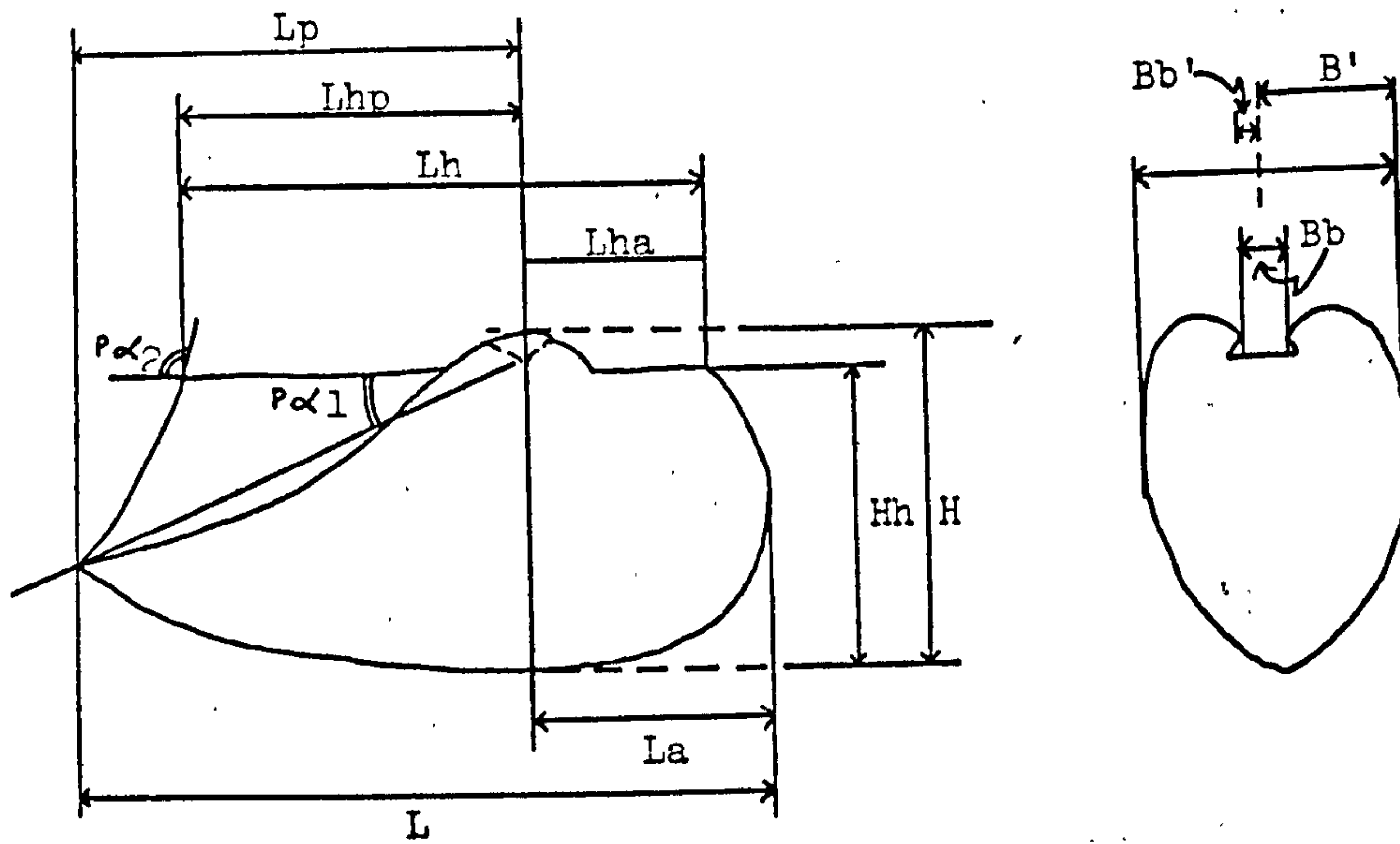


Figure 3.2

Dimensions in Arcacea and Pteriacea. The symbols are used in tables of measurements in the text.

Key:

L Maximum length
 La Length of anterior
 Lp Length of posterior
 H Maximum height
 Hh Height of hinge
 Lh Length of hinge
 Lha Length of anterior of hinge
 Lhp Length of posterior of hinge

B Breadth (two valves)
 B' Breadth (single valve)
 Bb Separation of beaks
 Bb' Horizontal separation of
 beak and hinge
 $P\alpha_1$ Posterodorsal angle
 $P\alpha_2$ Posterior area angle

Although Nowell (in Moore Ed., 1969, pp. N257-258) states that the valve margins of the Grammatodontinae are closed, there is evidence here in Cosmetodon that a weak byssal gape may be present.

Genus GRAMMATODON Meek and Hayden, 1861

Gerasimov (1955, pp 45-46) constructed a key for identifying Upper Jurassic species of 'Parallelodon' from the Russian Platform. His interpretation of Parallelodon includes forms regarded here as belonging to Grammatodon subgenera Grammatodon and Cosmetodon. The majority of the species he describes are found in the Spilsby Sandstone. As this key is useful and referred to in the discussions below, a translation is included here:

- | | |
|--|----------------------------|
| 1. Shell low, distinctly elongate | 2 |
| - Shell relatively high, rhomboidal, triangular | |
| or trapezoidal in outline | 6 |
| 2. Shell length not less than 3x the height | <u>P. productum</u> |
| - Length 1½-2x greater than height | 3 |
| 3. Surface folded with distinct radial sculpture | 4 |
| - Radial sculpture indistinct or absent | 5 |
| 4. Shell relatively large, up to 60mm in length | <u>P. keyserlingii</u> |
| - Length of shell not more than 35mm | <u>P. lutigini</u> |
| 5. Posterior end of shell somewhat projecting | <u>P. rouillieri</u> |
| - Shell distinctly tapering towards posterior | <u>P. compressiusculum</u> |
| 6. Sculpture radial and concentric | <u>P. pictum</u> |
| - Sculpture only concentric | <u>P. schourovskii</u> |

Grammatodon (Grammatodon) schourovskii (Rouillier & Vossinsky) 1847

Plate 1, figures 1a-c, 2a-d, 3, 4, 5, 6a-c, 7a-c.

- *.1847 Cucullaea Schourovskii sp. nov. Rouillier & Vossinsky, p.428.
- .1848 Cucullaea Schourovskii Rouillier & Vossinsky, p.287,
pl. H, fig. 39.
- .1866b Cucullaea Schtschourowskii Rouillier; Eichwald, pp. 565-566.
- .1905 Macrodon Schourovskii (Rouillier); Borissjak, pp. 14, 48,
pl. 2, figs. 10-12.
- .1905 Macrodon Schourovskii (Rouillier) var. a ssp. nov.
Borissjak, pp. 12, 48, pl. 2, fig. 13.
- .1905 Macrodon Schourovskii (Rouillier) var. b ssp. nov.
Borissjak, pp. 13, 48, pl. 2, fig. 14.
- 1911 Macrodon schourovskii (Rouillier); Ravn, p. 496
- 1930 Parallelodon (Grammatodon) schourovskii (Rouillier);
Arkell, p. 340.
- .1936 Parallelodon schourovskii (Rouillier); Spath, p. 113,
pl. 43, fig. 2, pl. 49, figs. 4,5.
- .1955 Parallelodon schourovskii (Rouillier & Vossinsky);
Gerasimov, p. 49, pl. 1, figs. 17, 18.
- 1974 Grammatodon schourovskii (Rouillier & Vossinsky);
Zakharov, p. 133.

Types. Rouillier and Vossinsky (1847) infer that there were several syntypes. Although two specimens were supposed to be figured with the original description (1847), the plate descriptions (1848, fig. 39A and 39B) indicate two views of a single specimen. These came from the 'étage à Ammonites virgatus' of the Moscow region and are believed lost

(Gerasimov, pers. comm. 1974).

Diagnosis. Shell relatively short, strongly inflated. Posterior obliquely truncate. Anterior not projecting beyond anterior of hinge line. Surface ornament dominantly comarginal growth lines.

Material. c240 specimens. 36 highly phosphatised specimens (SRAK), from the Coprolite bed, Speeton Clay, ?Middle Volgian, Speeton, Yorks. c200 specimens (SRAK) from the basal Spilsby nodule bed, Middle Volgian, Nettleton, Lincs. 6 specimens (SMC) from the basal conglomerate of the Lower Greensand of Upware, Brickhill and Potton, Beds.

Description. Shell relatively short, strongly inflated. Length usually 20-25mm, height 12-15mm. Commissural outline trapezoidal, with short rounded anterior and obliquely truncate posterior, posterodorsal angle c110-120°. Anterior margin drops vertically and then swings in a posterior direction from the hinge line and gently curves into the weakly convex ventral margin. The umbo is low and blunt, with small, sharp, weakly prosogyrate beaks which overhang the broad ligamental area. The beaks are situated about one third the length of the hinge line from the anterior. The flank of the shell is ornamented by fine growth lines which become exaggerated in old age near the commissure. On some specimens feeble radial thread-like ornament may be seen. The posterior carina is only marked in the juvenile stages and becomes increasingly rounded after 4-5mm from the beak. The posterior area is ornamented as on the flank; it is flat to slightly concave near the umbo. The hinge line is strong. 5-6 short opisthocline anterior teeth. 7-8 posterior teeth, elongate to short, some recurved towards the venter. Margin smooth, lip thickened. Adductor scars weakly impressed, pallial line defining inner margin of thickened lip. There may be a weak byssal gape

near the anterior of the ventral margin.

Discussion. Rouillier and Vossinsky (1948) figured a relatively elongate specimen of G. schourovskii. Borissjak (1905) attempted to illustrate the variation in morphology of the species by erecting subspecies a and b, but these are difficult to interpret because of the fragmentary material, or preservation as internal moulds. Little can be added, for similar reasons, from the specimens described here from the Spilsby Sandstone and Speeton Clay. Spath's material (1936) from the Middle Volgian of East Greenland shows most clearly the delicate radial ornament that may be present in the species. Gerasimov (1955) figured specimens from the Middle Volgian of the Moscow region that are extremely close to the original figured specimen of Rouillier and Vossinsky (1948).

Grammatodon minima (Leckenby 1859) (= Macrodon pictum Milaschewitsch, 1881 from the Callovian to Oxfordian, redescrbed by Duff, in press), is distinguished by its shortness and the finely cancellate ornament. Young specimens of G. (C.) compressiusculum (Rouillier & Vossinsky) are less inflated, more elongated in a posteroventral direction, and the anterior margin projects beyond the anterior of the hinge line; the adult is much larger and dentition is much finer than in G. schourovskii. 'Arca' longipunctata Blake (1875) from the Lower Kimmeridgian of Lincolnshire has a more prominent anterior region. G. spilsbiensis sp. nov. is similar in outline to G. schourovskii, but has a much thinner shell and dominant radial ornament.

Occurence. Middle Volgian of the Spilsby Sandstone and the Coprolite Bed, Speeton Clay in eastern England; the Hartwell Clay of south central England; East Greenland, the Moscow region and the North Urals.

Grammatodon (Grammatodon) spilsbiensis sp. nov.

Plate 1, figure 8a-e.

Holotype. SRAK, IG. 1704, internal and external moulds of a single right valve from a loose concretion of Lower Spilsby Sandstone containing Subcraspedites sowerbyi, S. preplicomphalus Zone, Upper Volgian, road cutting 1km north of Spilsby, Lincs.

Diagnosis. Shell relatively short, strongly inflated. Posterior margin truncate; anterior margin projecting and rounded. Ornament dominantly radial.

Description. Shell relatively short, strongly inflated. Commissural outline trapezoidal with obliquely truncate posterior margin, posterodorsal angle $cl30^\circ$. Anterior margin projecting weakly beyond anterior of hinge line, bluntly rounded. Ventral margin straight. Posteroventral junction rounded. Umbo bluntly rounded and projecting. Beak small, pointed and weakly prosogyrate, situated one third the length of the hinge line away from the anterior of the hinge. Flank and posterior area ornamented by fine closely set strong radial threads. These are single over most of the flank, but near to the anterior and posterior close to the margin, they branch dichotomously, which is a feature by which secondary threads may be introduced. The posterior carina is weakly defined near the umbo, but in later stages is a broadly rounded zone separating the flank from the relatively flat posterior area. Commarginal ornament is restricted to extremely fine growth lines, subordinate to the radial ornament. 3 major growth halts are visible. The interior of the shell is smooth, the hinge line narrower than in G. schourovskii and the teeth more delicate. The posterior laterals are straight and horizontal. The adductor scars

are obscure. Margin not thickened.

Dimensions. (See Figure 3.2)

	L	Lh	Lha	La	H	Hh	B	Bb	α_1
IG.1704	27	17	6	9	16	14	7'	1'	130°
Holotype									

Discussion. G. spilsbiensis is represented by a single specimen, with distinctive shape and radial ornament stronger than that occurring on previously described species. G. minima (Leckenby) is shorter, has a more prominent posterior carina, less strong radial ornament and less projecting anterior margin. G. compressiusculum (Rouillier & Vossinsky) is more elongate with coarser, flatter radial ornament. G. schourovskii lacks the strong radial ornament.

Occurrence. Spilsby Sandstone, Upper Volgian, eastern England.

Subgenus COSMETODON Branson, 1942.

Grammatodon (Cosmetodon) productum (Rouillier & Vossinsky) 1847

Plate 1, figures 9a-d, 10a-c, 11a-c, 12.

- .1847: Cucullaea concinna de Buch; Rouillier & Vossinsky, pp.425-426.
- *.1847 Cucullaea producta sp. nov. Rouillier & Vossinsky, pp. 426-427.
- .1848 Cucullaea concinna de Buch; Rouillier & Vossinsky, p. 286,
pl. H, fig. 36.
- .1848 Cucullaea producta Rouillier & Vossinsky, pp. 286-287,
pl. H, fig. 37.
- .1850 Arca producta Rouillier; d'Orbigny, p. 369.
- 1866b Cucullaea producta Rouillier; Eichwald, pp. 558-559.
- .1905 Macrodon lutugini sp. nov. Borissjak, pp; 5-7, 44-45,
pl. 1, figs. 10-12.

- .1905 Macrodon productum (Rouillier); Borissjak, pp. 7, 45,
pl. 1, figs. 14, 15.
- 1930 Parallelodon (Beshausenia) lutugini (Borissjak);
Arkell, p. 339.
- 1930 Parallelodon (Beshausenia) productum (Rouillier);
Arkell, p. 339.
- .1936 Parallelodon sp. nov.? aff. keyserlingi (d'Orbigny);
Spath, pp. 112-113, pl. 43, fig. 3, pl. 44, fig. 6,
pl. 45, fig. 2, pl. 49, fig. 3.
- .1955 Parallelodon lutugini (Borissjak); Gerasimov, p. 47,
pl. 1, figs. 8, 9.
- .1955 Parallelodon productum (Rouillier & Vossinsky); Gerasimov,
p. 47, pl. 1, figs. 15, 16.
- ?1964 Parallelodon cf. lutugini (Borissjak); Wellnhofer, pp.
30-31, pl. 1, figs. 22-23.
- .1969 Parallelodon lutugini (Borissjak); Gerasimov, p. 55,
pl. 4, figs. 1,2.

Types. Rouillier & Vossinsky figure 2 syntypes (1848, pl. H, figs
37A,B and 37C,D) which are believed lost (Gerasimov, 1974 pers. comm.)

They came from the 'étage à Ammonites virgatus' Khoroschovo, Moscow.

Selection of a neotype must await study of topotype material.

Diagnosis. Shell elongate, trapezoidal to wedge shaped. Posterior deep.
Anterior margin not projecting but sloping in posterior direction. Flank
ornament of fine radiating ribs. Weak median sulcus.

Material. 10 specimens (SRAK) Basal Spilsby nodule bed, Middle Volgian,
Nettleton, Lincs.

Description. Adult shell of medium size, elongate, trapezoidal to wedge shaped and inflated. Anterior very short, shallow. Anterior margin not projecting, but sloping in posterior direction. Posterior deep, posterior margin not clearly seen in Spilsby material, but believed to be obliquely truncate. Ventral margin indented by weak median sulcus. Umbro broadly rounded, low. Beak small, slightly overhanging the large ligamental area. Flank ornamented by fine radiating ribs, with subordinate commarginal growth lines. Posterior carina broadly rounded, posterior area relatively flat. Internally smooth. Hinge narrow, posterior teeth extremely elongate, median and anterior teeth short and ventrally convergent. Umbonal cavity very shallow. A weak but definite gape appears on the ventral margin associated with the median sulcus suggesting byssal attachment.

Discussion. It has been necessary to unite several 'species' of Cosmetodon under G. (C.) productum because of the considerable variation in morphology inherent in the species. Even amongst the fragmentary material from the basal Spilsby nodule bed there can be shown limited variation. Arkell (1930, p. 346) has indicated the extreme range of morphology that can exist within single species in the Arcacea.

C. (G.) productum was originally described and figured alongside Cucullaea concinna de Buch (non C. concinna Phillips) by Rouillier & Vossinsky (1847, p. 427); both came from the 'étage' a Ammonites virgatus. C. productum was differentiated from C. concinna because it was

- 1) more elongate;
- 2) the posteroventral angle was not elongate;
- 3) the posterior wing margin was not indented; and
- 4) the ventral and dorsal margins were not parallel.

Statements 1-3 hold as far as the figured specimens show, however statement 4 can be dismissed immediately as both sets of figures taper towards the anterior. When further figured material is examined e.g. Borissjak (1905) and Gerasimov (1955), the distinguishing features merge into one another. The true Arca concinna (Phillips) is a Callovian Grammatodon ss. which is redescribed by Duff (in press).

Borissjak (1905) illustrated G. (C.) productum under the genus Macrodon. The two figured specimens show a low umbo, gentle tapering of the shell, a weak median sulcus and a straight to slight concave posterior wing margin. His material is labelled Lower Volgian from Khoroschovo and Mnevniki and may correspond therefore to Middle Volgian as interpreted here. Also from the 'Lower Volgian' of Khoroschovo, Borissjak described a new species M. lutugini. His illustrated syntypes show slightly more prominent umbones than in his figures of M. productum, but they clearly fit into the range of variation of the species. His varieties a-c cannot be safely compared to other material because of their generally poor state of preservation. Arkell (1930) has placed both these figured species of Borissjak within Parallelodon (Beshausenia).

Spath (1936) figured G. (C.) productum from the Middle Volgian of East Greenland as Parallelodon sp. nov? aff. keyserlingi (d'Orbigny). The specimens are closely comparable in shape to the specimen figured here (pl. 1 fig. 9) which appears to show that the anterior in mature shells is relatively deeper than in juveniles.

More recently, Gerasimov (1955) figured various members of the Grammatodontinae as species of Parallelodon. A translation of the key he used to differentiate species appears above under the discussion

of the genus Grammatodon. He distinguished 3 'species', here referred to G. (Cosmetodon), namely P. keyserlingii, lutugini and productum. It would appear from his figured specimens that the observations on P. productum were based on internal moulds and therefore the actual shell length/height ratio would be well below the quoted value of 3 in actual shell specimens. Although only a relatively small number of specimens of G. (C.) productum have been collected from the Spilsby Sandstone, it is a variable assemblage and the individuals can be allocated to each of the 'species' P. keyserlingii, lutugini and productum as interpreted by Gerasimov, but cannot be specifically separated from each other. All the specimens which have the proximal end of the posterior lateral teeth, show them to be meeting the dorsal margin of the hinge plate and therefore correspond to the subgenus Cosmetodon Branson (1942) of which G. (C.) keyserlingii is the type species.

It is not possible here to provide a full review of the relationship between the true (Oxfordian) G. (C.) keyserlingi (d'Orbigny) and G. (C.) productum. It appears that G. keyserlingi may be distinguished by being more conspicuously alate and by having a distinct concave margin to the wing. The two species are probably intergradational with G. keyserlingii giving rise to G. productum.

G. (C?) rouillieri (Lahusen 1883) from the Lower Oxfordian of the Russian Platform differs from G. (C.) productum by having commarginal ornament more prominent than radial and the posterior of the shell has a distinct ventral swing, while G. (C.) compressiusculum (described below) is differentiated by lacking the median sulcus and having more cancellate ornament.

The figures of Parallelodon lutugini (Borissjak) from the Upper Volgian of the Russian Platform (Gerasimov 1969) and of Parallelodon cf. lutugini (Borissjak) from the Middle Tithonian of Bavaria (Wellnhofer, 1964) may represent G. (C.) productum, but the figured specimens are not sufficiently distinct to be certain.

Occurrence. Middle Volgian of eastern England, East Greenland; Middle and Upper Volgian of the Russian Platform and possibly from the Middle Tithonian of southern Germany.

Grammatodon (Cosmetodon) compressiusculum (Rouillier & Vossinsky) 1847.
Pl. 1, figs. 13a-c, 14a,b, 15a-c, 16, 17a,b.

- *.1847 Cucullaea compressiuscula sp. nov. Rouillier and Vossinsky,
p. 427.
- .1848 Cucullaea compressiuscula Rouillier and Vossinsky,
pp. 287, pl. H, fig. 38.
- .1866b Cucullaea compressiuscula Rouillier; Eichwald, pp. 564-565.
- .1905 Macrodon compressiuscula (Rouillier); Borissjak, pp. 13,
48-49, pl. 2, fig. 7.
- .1930 Parallelodon (Beshausenia) compressiusculum (Rouillier);
Arkell, p. 339.
- .1955 Parallelodon compressiusculum (Rouillier); Gerasimov,
pp. 47-48, pl. 2, figs. 1-4.
- 1974 Grammatodon compressiusculum (Rouillier and Vossinsky);
Zakharov, p. 133.

Type. Rouillier and Vossinsky figured one specimen which appears to be the holotype by monotypy. It is untraced, believed lost (Gerasimov, 1974,

pers. comm.) and came from the 'étage à Ammonites virgatus', Khoroschovo.

Material. 25 specimens (IGS and SRAK). Basal Spilsby Nodule Bed, Middle Volgian, Lincolnshire.

Diagnosis. Shell small to medium sized, elongate, obliquely trapezoidal. Surface ornament of relatively flat radial ribs, with broad commarginal growth lines.

Description. Adult shell of small to medium size, moderately to strongly inflated, overall length usually 20-40mm. Commissural outline obliquely trapezoidal with slight postero-ventral attenuation. Anterior short. Anterior margin weakly inflated beyond anterior of the hinge line. Posterior elongate. Posterior margin obliquely truncate, with posterodorsal angle c140°. Ventral margin relatively straight with gently rounded junction with the anterior margin and with a slight ventral swing near the posterior before rounding onto the posterior margin. Umbo small, rounded and slightly projecting. Beak small and situated about one quarter the length of the hinge away from the anterior of the hinge line, weakly prosogyrate and overhanging the long ligamental area. Surface ornament of flat broad ribs about 1mm at the widest and separated by much finer grooves. There is similar commarginal ornament and where radial and commarginal grooves meet, a punctation appears. This ornament does not appear clearly in marginal areas of large specimens where irregular growth lines predominate. The flank is separated from the posterior area by a poorly defined change of slope to the flatter posterior area. The flank ornament gradually dies to radial rows of fine pits on the posterior area. The hinge line is strong. Anterior teeth are slightly curved and become almost horizontal close to the anterior margin.

Posterior laterals very elongate and only slightly recurved. Internally the shell is smooth but there may be traces of fine radial threads. The adductor scars are obscure. Shell moderately thin and not thickened at lip.

Discussion. Rouillier and Vossinsky's (1848) figure of the type of G. (C.) compressiusculum differs from the Spilsby Sandstone specimens illustrated here in that the ligamental area appears to be very short. However the subsequent figures of material from the Russian Platform by Borissjak (1905) and Gerasimov (1955) indicate comparable ligamental areas to the Spilsby Sandstone material.

G. (C.) compressiusculum differs from the Spilsby species of Grammatodon ss. by its greater length, the position of the beak closer to the anterior of the hinge line, the more projecting anterior margin and finally the cancellate ornament which also differentiates it from G. (C.) productum.

Although G. compressiusculum is referred to the subgenus Cosmetodon, because the overall shape of the shell is relatively elongate and the proximal ends of the posterior pseudolateral teeth meet the ventral border of the hinge line, the precise position is probably between Grammatodon ss. and Cosmetodon ss., though closer to the latter. These subgenera may not be separate lineages but part of a plexus.

Occurrence. Middle Volgian of Eastern England, the Moscow basin and the North Urals.

Family	CUCULLAEIDAE Stewart, 1930
Genus	CUCULLAEA Lamarck, 1801
Subgenus	DICRANODONTA Woods, 1899 emend. Kelly herein

Type species. Cucullaea (Dicranodonta) donningtonensis Keeping, 1883, by original designation. However Woods misidentified the species and an application has been made to the ICZN (Appendix 5) to designate the species that was before Woods, here redescribed as C. (D.) benniworthensis sp. nov.

Diagnosis. Small to medium sized cucullaeid with subhorizontal pseudolateral teeth in specimens up to about 25mm length, the teeth becoming increasingly dorsally convergent in larger specimens. External shell surface ornamented by strong radial ribs which are usually inverted v-shaped in cross section, with subordinate much finer radial riblets in between, usually 3-6 in number. Intervals between the strong radial ribs may be flat in the anterior and posterior regions, but more rounded in the umbonal and mid-flank regions. Internally the shell is smooth, but there are strong marginal denticulations on the ventral border which correspond to the major radial ribs. The posterior adductor scar is not situated on a raised plate.

Discussion. C. (Dicranodonta) is redefined here to embrace certain mesozoic cucullaeids characterised by strong radial ribs and marginal denticulations which differentiate it from the finely ribbed Cucullaea (Cucullaea) which Newell (in Moore Ed. 1969) restricts to the recent of the Indo Pacific. C. (Idonearca) Conrad (1862) is almost smooth. Lopatinia Schmidt (1872b) from the Lower Cretaceous of the north Urals has a similar dentition and the finer radial ornament of Dicranodonta but lacks the coarser radial ornament and the marginal denticulations. L. (Pseudocucullaea) Solger (1903) from the Upper Cretaceous of West Africa and South America is unornamented. Megacucullaea Rennie (1936) from the late Jurassic of

south and east Africa and India has much fewer and coarser radial ribs, c.5-6 in number.

As type species of Dicranodonta, Woods (1899) designated Cucullaea donningtonensis Keeping. His original diagnosis of Dicranodonta states: 'Shell stout, subquadrate or rounded. Hinge area broad. Hinge plate large, curved, central teeth transverse; lateral teeth long, curved ventrally, nearly parallel, often bifurcating. No posterior adductor plate.' This diagnosis clearly refers to some robust Claxby Ironstone Cucullaea which Woods identified as C. donningtonensis but which are regarded here as specifically distinct and renamed C. (D.) benniworthensis sp. nov. To accord with Woods' ideas, an application has been made to the ICZN to designate C. (D.) benniworthensis as the type species of Dicranodonta under Article 70(a) of the Code (Stoll et al. 1964) (See Appendix 5). The holotype of C. donningtonensis came from the reworked deposits of Upware (as Woods realised) and is placed in synonymy with C. vagans Keeping, also from Upware.

Woods placed C. vagans outside his concept of Dicranodonta and he made no attempt to compare the species with his Claxby 'D. donningtonensis' so obviously did not consider them to be closely related. However, more detailed study of C. vagans suggests that both should be regarded as members of the same subgenus. As redefined here, Dicranodonta embraces all the material which Woods originally included in the subgenus but includes also C. vagans. The emended diagnosis stresses features which Woods apparently regarded as of little significance in differentiating subgenera. Indeed, Woods' diagnosis would place Dicranodonta in Lopatinia Schmidt. Woods (1899) stated that 'the form described by

Keyserling (1846) and by F. Schmidt (1872) as Pectunculus petschorae probably belongs to this subgenus [i.e. Dicranodonta]. The latter author was inclined to regard it as the type of a new subgenus'. Unfortunately Woods only referred to the 1872a paper of Schmidt, but later the same year, Schmidt (1872b) published the name Lopatinia for this and a related species. Woods does not refer to this paper, but in 1914 he does refer to the works of Solger (1903) and Schmidt (1904) in which the genera Pseudocucullaea (1903) and Lopatinia Schmidt (1872b) are discussed, and indicates that further research should be done on Dicranodonta. As Woods (1899) believed that the figures of P. petschorae were probably the same as his subgenus Dicranodonta, it seems likely that had Woods been aware initially of the 1872b Schmidt paper, Dicranodonta would not have appeared and Lopatinia would have been used. However, Lopatinia (type species P. petschorae by subsequent designation of Maury 1930) has a smooth margin and the external ornament is of fine radial elements without the coarse radial elements of Dicranodonta.

As redefined, Dicranodonta excludes some forms previously placed in this subgenus (e.g. D. sibirica (d'Orbigny) by Borissjak 1905) which fit better into Lopatinia.

Newell (in Moore Ed. 1969) sinks Dicranodonta into the synonymy of Cucullaea s. l. with Lopatinia as a separate genus embracing the subgenera Lopatinia s. s. and Pseudocucullaea. Nicol (1954) had preferred to place Dicranodonta and Lopatinia amongst others as separate subgenera of Cucullaea. Until there is further understanding of Upper Jurassic and Lower Cretaceous cucullaeids, Dicranodonta is provisionally replaced here as a subgenus of Cucullaea.

Occurrence. Middle Volgian to Valanginian and ?Hauterivian of eastern England, Middle Volgian to Ryazanian of East Greenland, Hauterivian of north west Germany. It may occur in the ?Middle Volgian of the Russian Platform.

Cucullaea (Dicranodonta) vagans (Keeping) 1883

Plate 2, figures 1a-d, 2a-c, 4a-c, 5a, b, 6, 7, 8, 9a-c, 10a, b,
12, 13, 14a, b.

- .1883 Cucullaea errans Keeping, pp33,34,36,65 (corrected to
C. vagans in errata; nom. nud.)
- v*.1883 Cucullaea vagans sp. nov. Keeping; pp. 151-152, pl. 8,
fig. 8.
- v.1883 Cucullaea donningtonensis sp. nov. Keeping, pp. 152-153,
pl. 8, fig. 9.
- v.1889 Cucullaea vagans Keeping; Woods, pp. 52-53, pl. 10,
figs 8-10.
- vp.1899 Cucullaea (Dicranodonta) donningtonensis Keeping; Woods,
pp. 54-55, non pl. 10, figs 11-14, pl. 11, figs. 1,2.
- .1924 Idonearca (Dicranodonta) vagans Keeping; Gillet, p.18.
- .1936 Dicranodonta groenlandica sp. nov. Spath, p. 177, pl.
41, figs. 11a-d.
- .1947 Dicranodonta cf. groenlandica Spath; Spath, pp. 39-40,
pl. 3, fig. 3, pl. 4, fig. 5.

Types. Keeping did not designate a holotype; however all the syntypes are preserved: SMC B.27515-27525 from the Black Grit nodules of Upware and SMC B. 27656-27657 from an erratic block of Spilsby Sandstone from Herrimere, Cambridgeshire. From this material SMC B. 27515 is selected

as Lectotype.

Diagnosis. Adult shell with maximum length 27mm. Exterior strongly ribbed. Posterior area weakly defined. Commissural outline suboval. Pseudolateral teeth subhorizontal.

Material. 200 specimens. Occasional to common in most facies of the Spilsby Sandstone, Roxham Beds and Runcion Beds, including reworked material of Upware and in erratic blocks.

Description. Adult shell medium sized with maximum length 27mm. Commissural outline obliquely ovate with inflated shell and projecting umbo subcentral with sharp overhanging orthogyrate beak. Anterior of shell shallower than weakly truncate posterior. Whole surface ornamented by c25 strong radial inverted v-shaped ribs with between 3 and 6 finer intermediaries. The grooves between the ribs may be rounded or flat bottomed, the latter being more prominent at the anterior and posterior where major ribs weaken and die out gradually. Commarginal growth lines may cut this ornament in a regular manner every 1mm or be completely irregular. The posterior carina is not well defined and the flank ornament passes over onto the posterior area without a break. The ligamental area is short and deep. The hinge line is straight and does not extend as far as the anterior and posterior margins. Internally the shell is smooth except for the ventral margin which bears denticulations that correspond to the major radial ribs. The anterior adductor scar is subcircular, while the posterior adductor scar is more ovate. There is no supporting buttress for the posterior adductor scar. Umbonal cavity is large. Pseudocardinal teeth short and dorsally convergent. Pseudolateral teeth subhorizontal.

Measurements.

	L	Lh	La	Lha	H	Hh	B	Bb	$\rho \propto 1$
SMC B. 27524	23	12	12	5	19	16	8'	2'	130
B.27526	24	13	11	6	20	18	9'	3'	135
B.27577	26	15	12	7	20	18	10'	2'	150

Discussion. While Cucullaea vagans has generally been regarded as a relatively small cucullaeid occurring in the Spilsby Sandstone, and in the reworked deposits of Upware, C. donningtonensis has generally been used for the relatively large cucullaeid common in the Claxby Ironstone and occasionally found in the upper part of the Spilsby Sandstone (e.g. Woods 1899). However the type specimen of C. donningtonensis as designated by Keeping (1883, pl. 2, fig. 4.) is an external mould from the same horizon of reworked phosphatised nodules at Upware as most of the syntypes of C. vagans, and I cannot separate specifically the casts taken from these moulds (pl. 2, figs. 2-4). Keeping recorded a single paratype of C. donningtonensis from the 'Lower Cretaceous Sands of Doddington' (misspelling of Donnington). The largest known specimen of C. vagans is illustrated here from the Spilsby Sandstone of Donnington (pl. 2, fig. 8) and although approaching the size of the typical large Claxby Ironstone forms, it differs from them by having a more rounded posterior area and smaller size. It is therefore necessary to transfer the familiar name of C. donningtonensis into the synonymy of C. vagans. The Claxby Ironstone form is renamed below as C. (D.) benniworthensis.

Spath (1936, 1947) figured and described Dicranodonta groenlandica from loose blocks on Aucella River and from the H. kochi beds of Southern Jameson Land, East Greenland. This material is supplemented

by the author's own collection (1973) from the Ryazanian of Hesteev. Although Spath states that this species differs from D. donningtonensis, he is clearly referring to the large specimens figured by Woods (1899) and not to the holotype of Keeping (1883). All this Greenland material (pl. 2 figs. 9, 10) corresponds exactly to the English C. vagans.

Dicranodonta pectunculoides (Trautschold) figured by Borissjak (1905) from the Callovian of Central Russia and D. mnienvnikensis from the Lower Volgian, can be confused superficially with C. (D.) vagans, but have the characteristic smooth margins and weaker surface ornament of Lopatinia. Arca sibirica d'Orbigny (1845) from the 'grès noirâtre, oxfordien,' of the north Urals, also figured more clearly by Borissjak (1905) and by Gerasimov (1955) from the Lower and Middle Volgian, is characterised by much weaker surface ornament consisting of alternating weak and slightly less weak radial ribs. The ventral margin is non-denticulate. All this Russian material is again referred to Lopatinia.

Borissjak (1905, pp. 32, 60, pl. 4, fig. 13) figured an internal mould of Dicranodonta sp. ind. which shows fine marginal denticulations, finer than those in the Spilsby Sandstone specimens. The umbonal infilling is also less prominent. The example from the 'Obere Wolga-Stufe, Worobjewo' may be Dicranodonta but without seeing the external ornament, it remains to be confirmed whether Dicranodonta occurs in Russia.

Occurrence. Middle Volgian to Ryazanian of eastern England and of East Greenland.

Cucullaea (Dicranodonta) benniworthensis sp. nov.

Plate 2, figures, 16a-d.

vp. 1899 Cucullaea (Dicranodonta) donningtonensis Keeping;

Woods, pp. 54-55, pl. 10, figs. 11-14, pl. 11, figs. 1-2.

.1923 Idonearca (Dicranodonta) donningtonensis Keeping;

Gillet, p. 18, text fig. 6.

.1948 Cucullaea (Dicranodonta) donningtonensis Keeping;

Wilson, pp. 55-56, fig. 19 H.

v.1962 Dicranodonta donningtonensis (Keeping); Castell, pl50,

pl 53, fig. 6.

Types. The holotype is designated as SMC B.11222, from the Claxby Ironstone, probably Valanginian, of Benniworth Haven, Lincs. It was originally figured by Woods (1899, pl. 10, fig. 11) and is refigured here, pl. 2, fig. 12. There are several hundred paratype specimens in the collections of IGS, BMNH and especially SMC and SRAK from the Claxby Ironstone and topmost Spilsby Sandstone of Lincolnshire.

Diagnosis. Adult shell length commonly 45-60mm. Pseudolaterals dorsally convergent. Rounded posterior carina with relatively flat posterior area and obliquely truncate posterior margin.

Description. Commissural outline trapezoidal with rounded anterior projecting slightly beyond anterior of the hinge line. Posterior margin steeply truncate. Ventral margin short and straight to slightly inflated. Deepest part of shell may be towards anterior or posterior. Umbo large, projecting, subcentral, inflated, generally broad but variable. Beak sharp overhanging and orthogyrate. Flank ornamented by about 25 strong

radial ribs separated by u-shaped to flat bottomed grooves bearing 4-6 finer radial riblets. Comarginal growth lines very subordinate, but become more prominent in late growth stages. Posterior carina is bluntly rounded, separating the flatter posterior area from the inflated flank. Very subdued flank style ornament appears on the posterior area. Ligament area is large. Hinge line relatively short. Hinge plate narrow at centre, but deeper at the anterior and posterior ends. Pseudocardinal teeth subvertical to dorsally convergent. Pseudolaterals very well developed, bifurcating and strongly dorsally convergent. Ventral margin with strong denticulations corresponding to the main ribs. Lip thickened. Anterior adductor scar subcircular, posterior scar more elongate.

Measurements.

	L	Lh	La	Lha	H	Hh	B	Bb	$p \times 1$
SMC B.11219	53	33	29	17	49	39	21'	5'	105
B.11220	55	32	30	17	46	33	21'	4'	110
B.11221	20	11	10	6	16	14	7'	1'	125
B.11222	51	30	27	16	43	35	20'	4'	115
B.11223	40	23	21	12	33	27	15'	2.5'	100

Discussion. The relationship between C. (D.) benniworthensis and vagans is discussed fully under the latter species. Juveniles of C. (D.) benniworthensis are indistinguishable from C. (D.) vagans, (e.g. pl. 2, fig. 15) apart from growth lines which become crowded at a larger size.

Lopatinia petschorae (Keyserling) as discussed by Schmidt (1872b), is smaller and bears more reticulate ornament. L. jennisae Schmidt although of comparable size has a more rounded commissural outline

and lacks the posterior truncation of C. (D.) benniworthensis.

Occurrence. Ryazanian to Valanginian (?Hauterivian) of the Upper Spilsby Sandstone to Claxby Ironstone of eastern England. Also one specimen in the E. Kemper Collection, from the Bentheim Sandstone, Hauterivian of north west Germany.

Order	MYTILOIDA Ferussac, 1822
Superfamily	MYTILACEA Rafinesque, 1815
Family	MYTILIDAE Rafinesque, 1815
Subfamily	CRENELLINAE Adams & Adams, 1857
Genus	MUSCULUS Rüdinger, 1798

Musculus (Musculus) fischerianus (d'Orbigny)

Plate 3, figs 11a, b, 12, 13a, b.

1843 Modiola pulcherrima (Roemer); Fischer, p. 134, (non Roemer 1836)

*.1845 Mytilus Fischerianus d'Orbigny, pp. 464-465, pl. 39, figs. 26-28.

1850 Mitylus Fischerianus d'Orbigny; d'Orbigny, p. 370.

1866b Modiola Fischeriana d'Orbigny; Eichwald, p. 536.

.1955 Musculus fischerianus (d'Orbigny); Gerasimov, pp. 135-136,
pl. 21, fig. 5.

Type Material. Murchison and Verneuil Collection, untraced: 'grès noirâtre de l'étage oxfordien', presumed Volgian, Khoroschovo, near Moscow.

Diagnosis. Adult shell of small to medium size, length about 18-25mm, moderately deep with weakly convex ventral margin. Posterior area covered with 20-28 fine but strong radiating ribs with also finer comarginal ribs.

Material. 8 specimens (IGS SRAK). Associated with Paracraspedites in erratic block of Lower Spilsby Sandstone, P. oppressus Zone, Middle Volgian, Leziate Sand Pit, Norfolk, and associated with S. sowerbyi, S. preplicomphalus Zone, Upper Volgian of Harrington and West Keal, Lincs.

Description. Adult shell of small to medium size, about 18-25mm in length and moderately deep and inflated. Shell strongly inequilateral with large posterior and extremely reduced anterior. Umbones low and rounded with very small prosogyrate beaks. The ventral margin is weakly convex. The anterior of the flank has about 7-9 rounded radial ribs which gently curve forwards as they close with the shell margin. The central part of the flank bears no radial ornament, just fine growth lines. The posterior part of the shell bears 20-28 fine radial ribs similar to those on the anterior with the addition of commarginal ornament giving a reticulate pattern in which the radial elements dominate. Internal features of the hinge and musculature are obscure.

Measurements.

	L	H	B	R ₁	R ₂
IG.2379	22	16.5	4.5'	-	20
1756	18.5	12	5.5'	9+	28
3390	25	11+	5'+	7	23

R₁ anterior radial ribs

R₂ posterior radial ribs

Discussion. D'Orbigny introduced M. fischerianus for the species that Fischer de Waldheim had originally referred to as M. pulcherrima Roemer. The former species has been recorded only from the Middle and Upper

Volgian, while the latter is normally found in the north European Neocomian and differs by having fine radial striae present upon the normally smooth mid flank region. M. autissiodorensis (Cotteau) (? = M. morinicus (de Lorient)) from the Kimmeridgian to Portlandian of north west Europe differs by reaching smaller adult size, is less deep, with a concave ventral margin and lacks the reticulate ornament. M. derehamensis sp. nov. described below has finer radial ornament, c35-44 radial ribs on the posterior, and lacks reticulate ornament. These Upper Jurassic forms may be derived from the Callovian-Oxfordian M. pulchra (Phillips) (= M. cancellata (Roemer)) which is slightly larger than M. fischeriana and has a finer radial ornament on the posterior of upwards of 50 ribs and a concave ventral margin. M. strajeskianus (d'Orbigny 1845), from the Upper Volgian of the North Urals, is a much larger musculid which is elongate (L c80mm) and shallow, while M. uralensis (d'Orbigny 1845) is also large (L c60mm) but is strongly recurved with a concave ventral margin. The latter species comes from the Lower to Upper Volgian of the North Urals.

Distribution. Middle Volgian of the Moscow region, Middle to Upper Volgian of the Spilsby Sandstone in eastern England.

Musculus (Musculus) derehamensis sp. nov.

Type Material. Holotype (IGS CE 6091) and about 25 Paratypes from one nodule (CE 5543) from ?Roxham Beds, ?Middle Volgian, Drainage Channel, Wormgay, Norfolk.

Diagnosis. Adult shell of small size, length 10 - 18mm. Posterior area ornamented by 35-44 radial ribs. No reticulate ornament.

Description. Adult shell of small size, length 10 - 18mm, moderately inflated. Shell strongly elongated towards posterior. Anterior very short. Relative depth about the same as in M. fischeriana. Umbo very low and rounded. Ventral margin weakly inflated. Posterior area ornamented by 35-44 very fine radial ribs, but no reticulate ornament. The flank is smooth with only very fine growth lines. The anterior bears about 13-16 fine curved ribs.

Measurements.

		L	H	B	R ₁	R ₂
Holotype	IGS CE 6091	18	10	5'	-	c42
Paratype	6092	16	11	4'	13	c42
"	6093	18	10	5'	-	35
"	6094	16	9	3'	-	39
"	6095	18	11	5'	-	c44

Discussion. M. derehamensis differs from M. fischerianus by its smaller size, the increase in the number of radial ribs on the posterior and the lack of reticulate ornament.

Distribution. ?Middle Volgian of eastern England.

Order	PTERIOIDA Newell, 1965
Suborder	PTERIINA, Newell, 1965
Superfamily	PTERIACEA Gray, 1847
Family	INOCERAMIDAE Giebel, 1852
Genus	ANOPAEA Eichwald, 1861

Discussion. The recognition of Anopaea in the Spilsby basin extends the

geographic distribution into north western Europe, and the stratigraphic range upwards into the Ryazanian.

Anopaea brachowi (Rouillier) 1849

Plate 3, figures 1a, b, 2-5.

- .1846 Inoceramus lobatus sp. nov. Auerbach & Frears, p.492, pl. 7,
figs. 1-3, (non Münster in Goldfuss & Münster 1835)
- *.1849 Inoceramus Brachowi sp. nov. Rouillier (in Rouillier &
Vosinsky), pp 348-349.
- .1850 Posidonomya lobata Auerbach & Frears; d'Orbigny, pp. 371-373.
- .1858 Inoceramus bilobus Auerbach & Frears; Trautschold, pp. 551-552,
fig. 9.
- .1861b Anopaea lobata Auerbach; Eichwald, pp. 301-302.
- 1866 Anopaea lobata Auerbach; Eichwald, pp. 480-481.
- ?1877 Inoceramus coneiformis d'Orbigny; Nikitin, pl15, pl. 3, fig. 8.
- .1955 Inoceramus (Anopaea) brachovi Rouillier; Gerasimov, pp. 104-105,
pl. 20, fig. 1.
- .1969 Anopaea brachovi (Rouillier); Gerasimov, p. 63, pl. 13, figs.
1-5, pl. 14, figs. 1-3.
- .1969 Anopaea brachovi (Rouillier); Cox (in Moore Ed.), p. N317,
fig. C47, 2.

Type Material. The type specimens of Inoceramus lobatus Auerbach and Frears came from Lidkarino, but are untraced. If necessary, a neotype may be selected from Gerasimov (1955).

Diagnosis. Anopaeid with smooth umbonal region. Gentle coarse commarginal undulations appear at a distance from the umbo.

Material. 11 specimens. 5 specimens (IGS), unhorizoned, Spilsby Sandstone, near Toynton All Saints, Lincs. 4 specimens (SRAK), Lower Spilsby Sandstone, S. lamplughii Zone, Upper Volgian, Nettleton, Lincs. 2 specimens (IGS), Mintlyn Beds, H. kochi Zone, Ryazanian, Abbey Station, West Dereham.

Description. Shell of moderate length, though in excess of 54mm. Moderately inflated. Umbones narrow and projecting with slightly recurved beaks, weakly prosogyrate and overhanging a deep lunule type structure. Hinge line short and straight, bearing large ligament pits. Shell surface smooth on umbonal region, but develops weak coarse commarginal folds about 15-20mm from the umbo which continue over the rest of the flank. The complete shell outline is not shown in English specimens, but one specimen (pl. 3 fig. 5) does show weakly the radial constriction separating the anterior lobe of the shell.

Discussion. Rouillier (in Rouillier and Vosinsky 1849) erected Inoceramus Brachowi as a nomen novum for Inoceramus lobatus Auerbach and Frears (1946), which is preoccupied by Münster (in Münster and Goldfuss 1835). Eichwald (1861b) made I. lobatus Auerbach & Frears the genotype of Anopaea by monotypy (Cox in Moore Ed. 1969).

The closely related A. sphenoidea (Gerasimov), described below, is distinguished by having stronger commarginal folds which cover the umbonal region as well as the flank. Gerasimov (1955) referred questionably the figure of I. cuneiformis (d'Orbigny) of Nikitin (1977) to A. sphenoidea. However Nikitin's figure shows a form too smooth to be A. sphenoidea, and it is here provisionally referred to A. brachowi. There are traces of radial ornament on the umbonal region.

Occurrence. Upper Volgian and Ryazanian of eastern England and the Upper Volgian of the Russian Platform.

Anopaea sphenoidea (Gerasimov 1955).

Plate 3, figures 6-8.

- .1845 Avicula cuneiformis sp. nov. d'Orbigny, p. 474, pl. 51, fig. 11.
- 1850 Avicula cuneiformis d'Orbigny; d'Orbigny, p. 372.
- 1866 Anopaea cuneiformis (d'Orbigny); Eichwald, pp. 482-484
- non1877 Inoceramus cuneiformis (d'Orbigny); Nikitin, p. 115, pl. 3, fig. 8
- *.1955 Inoceramus (Anopaea) sphenoideus sp. nov. Gerasimov, pp. 105-106,
pl. 20, figs. 2-5.
- .1969 Anopaea sphenoidea Gerasimov; Gerasimov,
pp. 63-64, pl. 15, figs. 1-8.

Type Material. Holotype: Gerasimov Collection, No. 1086, Kashpurites fulgens Zone, Upper Volgian, Kamennik, Yaroslav District, figured by Gerasimov (1955, pl. 20, fig. 2). 3 paratypes are also figured on the same plate (figs. 3-5) from the K. fulgens and G. catenulatum Zones of the Yaroslav and Moscow districts. Other paratypes may exist.

Diagnosis. Anopaeid with strong commarginal folds present on the umbonal and flank regions of the valve.

Material. 6 specimens, all associated with S. preplicomphalus Zone ammonites, Upper Volgian in the Lower Spilsby Sandstone of West Keal (3 specimens, SRAK), 1km north of Spilsby (1 specimen, SRAK) and in erratic blocks from Leziate (2 specimens, IGS).

Description. The Spilsby material is not well preserved in the marginal

regions. The shell reaches medium size, though may exceed 50mm length. Equivalve and moderately inflated. Umbones with small projecting beaks overhanging lunule type structure (on internal mould). Hinge line straight, with small ligament pits. Umbo and flank ornamented with coarse undulating commarginal folds which delineate the anterior lobe of the flank which is not clearly visible.

Discussion. Gerăsimov (1955) introduced A. sphenoidea as a nomen novum for Avicula cuneiformis d'Orbigny (1845), as this species was an inoceramid and therefore preoccupied by Inoceramus cuneiformis d'Orbigny (1843), a species from the Turonian of the Yonne.

A. sphenoidea differs from A. brachowi by having coarse commarginal folds on both the umbo and flank. A. sphenoidea appears to be the direct ancestor of A. brachovi, and occurs in the lower part of the Upper Volgian in both eastern England and on the Russian Platform. A. brachowi appears in both areas in the upper part of the Upper Volgian and continues into the Ryazanian in eastern England.

Occurence. Lower part of the Upper Volgian in eastern England in the Russian Platform.

Superfamily PECTINACEA Rafinesque, 1815

Family OXYTOMA Ichikawa, 1958

Genus ARCTOTIS Bodylevsky, 1960

Discussion. The occurrence of Arctotis in the Spilsby Sandstone extends the geographic distribution of the genus from the Jurassic-Cretaceous (Lias-Valanginian) of northern Siberia, into the Middle and Upper Volgian of

eastern England.

Arctotis intermedia Bodylevsky (1960)

Plate 3, figure 14.

*1960 Arctotis intermedia Bodylevsky, p. 44, pl. 7, figs 1, 2.

.1966 Arctotis intermedia Bodylevsky; Zakharov, pp. 24-28, pl. 3,
figs. 7-12.

Type Material. Holotype, Museum of Leningrad Institute of Mining,
No. 5/234, D. maximus Zone, Lower Volgian, R. Kamenayar, northern Taimyr,
Siberia.

Diagnosis. Shell small, ornamented by strong regular radial ribs and weak
commarginal lamellae.

Material. 3 specimens. 2 specimens (SRAK, IGS), in erratic boulders of
Lower Spilsby Sandstone, P. oppressus Zone, Middle Volgian, Leziate,
Norfolk. 1 specimen (SRAK), Lower Spilsby Sandstone, S. preplicomphalus
Zone, Upper Volgian, West Keal, Lincs.

Description. The three specimens have small shells of length 5-7mm.
They are all left valves which are strongly inflated. Outline subcircular
with short straight hinge on moderately developed posterior auricle and
weakly developed anterior auricle. Umbo feebly projecting with small
beak. Ornament of c24 regular radial ribs with weak commarginal lamellae.
Interior of left valve and whole of right valve not seen.

Measurements.

	L	La	Lh	Lha	Hh	B'
SRAK IG.2501	7	3	4	1	7+	3

Discussion. Although the Spilsby specimens are small, they correspond almost exactly to the figured Russian material, especially to Zakharov (1966) pl. 3, fig. 8.

Occurrence. Lower Volgian of northern Siberia and Middle and Upper Volgian of eastern England.

Family ENTOLIIDAE Korobkov, 1960.

Discussion. In a recent review of European Lower Cretaceous entoliids Dhondt (1972) attempted to distinguish the left and right valves of Entolium. Unfortunately there is confusion in her diagnosis of the genus and in the description of E. orbiculare. I have discussed this problem with Dhondt and we agree on the differentiation of the valves outlined in the description below of E. orbiculare.

Entolium (Entolium) orbiculare (J. Sowerby) 1817

Plate 4, figures 1 - 10.

- *.1817 Pecten orbicularis sp. nov. J. Sowerby, p. 193, pl. 86.
- .1843 Pecten numularis sp. nov. Fischer, pp. 135-136, pl. 5, fig. 4
- .1845 Pecten nummularis Phillips; d'Orbigny, pp. 475-476, pl. 41, figs. 20-23.
- .1846 Pecten nummularis Phillips; Keyserling, p. 296.
- .1846 Pecten demissus Bean; Keyserling, p. 296.
- .1861a Pecten solidus sp. nov. Trautschold, pp. 76-77, pl. 6, fig. 4.
- .1861a Pecten solidus Trautschold var. lamellosus nov. Trautschold, pp. 77-78, pl. 6, fig. 5. (non Sowerby 1819)
- .1861b Pecten demissus Bean var. normalis nov. Trautschold, pp. 268-269, pl. 7, fig. 4.

- .1861b Pecten demissus Bean var major nov. Trautschold, pp. 268-269.
pl. 7, fig. 2.
- .1862 Pecten nummularis (Phillips); Eichwald, pp. 375-376.
- .1862 Pecten orbicularis Sowerby; Eichwald, pp. 375-376.
- .1863 Pecten nummularis Phillips; Trautschold, p. 393.
- .1865 Pecten nummularis Phillips; Trautschold, p. 14, pl. 3, fig. 2.
- .1866 Pecten nummularis Phillips; Trautschold, p. 135.
- .1866a Pecten orbicularis Sowerby; Eichwald, p. 260.
- .1866a Pecten nummularis Phillips; Eichwald, p. 248.
- .1866b Pecten orbicularis Sowerby; Eichwald, pp. 423-426.
- .1866b Pecten Nilssoni Goldfuss; Eichwald, pp. 422-423.
- .1868 Pecten orbicularis Sowerby; Eichwald, pl. 20, fig. 4.
- ? .1868 Pecten Nilssoni Goldfuss; Eichwald, pl. 20, fig. 5.
- .1872a Pecten demissus Bean; Schmidt, p. 162.
- .1883 Pecten orbicularis Sowerby var. magnus nov. Keeping, p. 106,
pl. 5, fig. 1.
- .1893 Pecten (Entolium) erraticus sp. nov. Fiebelkorn, p. 400, pl. 14,
fig. 12.
- p.1900 Pecten Germanicus sp. nov. Wolleman pp 41-44 pl. 8, figs. 14-19
only, non. fig.
- pv.1903 Pecten (Syncyclonema) orbicularis Sowerby; Woods, pp. 145-152,
pl. 27, figs. 1-3, 5-14 text fig. 1, only, non. fig. 4,
- .1908 Pecten (Entolium) gothicus sp. nov. Krause, pp. 256-258,
pl. 4, figs. 6-7.
- ?1911 Pecten (Entolium) demissus Bean; Ravn, pp. 463-464, pl. 33,
fig. 8.
- 1911 Pecten (Entolium) erraticus Fiebelkorn?; Ravn, pp. 464-465.

- pl1917 Pecten demissus Goldfuss; Borissjak & Ivanoff, pp. 3-5,
pl. 1, figs. 8, 10, 18 only.
- .1931 Pecten (Entolium) nummularis d'Orbigny; Sokolov & Bodylevsky,
pp. 51-52, pl. 8, fig. 1.
- .1931 Pecten (Entolium) orbicularis Sowerby; Sokolov & Bodylevsky,
pp. 52-53, pl. 4, fig. 2.
- .1936 Entolium nummularis (Fischer); Spath, pp. 103-104, pl. 41,
figs. 9, 10, pl. 42, fig. 11.
- .1936 Entolium sp. Spath, p. 104, pl. 45, fig. 1.
- .1947 Entolium nummularis (Fischer); Spath, pp. 37-38, pl. 5,
figs. 5, 6, 9.
- .1953 Entolium cf. orbicularis (J. Sowerby); Donovan, p. 96, pl. 24,
fig. 2.
- ?pl1955 Entolium demissum (Phillips); Gerasimov, pp. 112-113, pl. 25,
figs. 4-6.
- .1955 Entolium erraticum (Fiebelkorn); Gerasimov, p. 113, pl. 25,
fig. 1.
- .1955 Entolium nummularis (Fischer); Gerasimov, pp. 113-114,
pl. 25, figs 2,3.
- .1958 Pecten (Entolium) cf. nummularis Orbigny; Bodylevsky &
Shulgina, pp. 64-65, pl. 19, figs. 1,2.
- .1958 Pecten (Entolium) aff. nummularis Orbigny; Bodylevsky and
Shulgina, p. 65, pl. 19, figs. 1,2.
- .1960a Entolium rossicum sp. nov. Glazunova, p. 48, pl. 8, fig. 1.
- .1960b Entolium cf. russicus Glazunova; Glazunova, p. 165, pl. 40,
figs. 1-3.
- ?1962 Entolium sp. II sp. indet. Pchelintseva, p. 72, pl. 12, fig. 4.

- .1962 Pecten (Entolium) nummularis d'Orbigny; Turbina, p. 69,
pl. 16, fig. 7.
- .1962 Pecten (Entolium) demissus Phillips; Turbina, p. 69, pl. 16,
fig. 9.
- ?pl966 Entolium demissum (Phillips); Zakharov, pp 33-35, pl. V,
figs. 4, 5, 6, (?non 1, 2) pl. VI, figs. 2-6.
- .1966 Entolium nummulare (d'Orbigny); Zakharov, pp. 35-38, pl. V,
fig. 3, pl. 6, figs. 2-6.
- .1969 Entolium numulare (Fischer); Gerasimov, pp. 64-65, pl 16,
figs. 3-5, 7, 9.
- .1969 Entolium erraticum (Fiebelkorn); Gerasimov, p. 138, pl. XVI,
fig. 6.
- .1971 Entolium (Entolium) orbiculare (J. Sowerby); Dhondt, pp. 8-27, Pl. 1,
figs. 1a, 1b.
- 1974 Entolium demissum (Phillips); Zakharov, pp.139-140.
- 1974 Entolium nummulare (Fischer); Zakharov, p. 140.

See Dhondt (1971 pp 8-14) for additional synonymy.

Type. Sowerby (1817) mentions a single specimen which came from the Upper Greensand of the Devizes canal. It was probably of Albian age, and not Cenomanian as suggested by Dhondt (1971, p. 14). The specimen has not been traced and must be presumed lost.

Diagnosis. Small to medium sized entoliid. Auricles subequal. Shell subcircular in outline and strongly compressed. Left valve smooth; right valve with concentric grooves 1-3mm apart, which may not persist into the more adult parts of the valve or which may be completely absent.

Material. Abundant in the sandy facies of the Spilsby Sandstone and Sandringham Sands, Middle Volgian to Ryazanian age.

Description. Shell suborbicular in outline and compressed. Adult length usually 25-45 mm with height equal to or just in excess of the length. Both valves are thin, equivalve and equilateral and although both are strongly compressed, the left valve may be slightly more inflated than the right. The beak and umbo coincide with a sharp umbonal angle which increases with growth, being about 105° in specimens of height 22mm and increasing gradually to about 120° in large specimens of height 50mm. The auricles are triangular and subequal and situated symmetrically adjacent to the umbo, with rounded dorsal corners projecting above the hinge axis. In the right valve the anterior auricle has a weak depression at its base, which appears to be a relict byssal notch. The anterior auricle of the left valve is slightly enlarged to cover the byssal notch in lateral aspect. The exterior of the flank is normally smooth and polished in the left valve, while the right valve can be covered by regular commarginal grooves set between 1 and 4mm apart. These grooves may extend only over the younger part of the right valve, leaving a smooth outer zone, or the grooves may be absent completely. Sometimes on exceptionally well preserved specimens, the fresh shell surface shows minute radial striae (pl. 4 fig. 3). In specimens that have been slightly corroded, both valves may have the individual growth increments etched out, giving the surface a much finer commarginal ornament than is found on the right valve.

Internally the shell is smooth. Radiating from the umbo are the heavily built auriculae crurae which extend almost as far as the base of the auriculae except in the right valve where the anterior auricula crura

extends beyond the anterior auricle. In the central and proximal part of the auricles is a raised 'bow-tie' shaped structure bearing teeth. (Text Figure 3.4). In the umbonal angle is a depressed resilifer set on a raised platform. Both of these structures comprise the hinge and ligamental area, and can be recognised by the striated surface of the parts of low relief upon which the ligament was attached. In the left valve the hinge axis runs along the crest of a horizontal pair of teeth that fade towards the beak, where they are interrupted by the apex of the resilifer. Below the horizontal teeth are two further pairs of weak, dorsally convergent chevronlike teeth, the inner pair marginal to the resilifer. In the right valve there is a corresponding set of teeth and sockets. There is a horizontal groove along the hinge axis, with a weak ventrally convergent pair of teeth above. Below the hinge axis are two further pairs of chevron shaped teeth with the ventral pair marginal to the resilifer.

A summary of the diagnostic features of the left and right valves of Entolium orbiculare is as follows:

Left	Right
Exterior always smooth	Exterior normally with commarginal grooves
Anterior auricula crura does not extend beyond base of anterior auricle	Anterior auricula crura extends beyond base of anterior auricle.
Hinge with horizontal ridge on hinge axis	Hinge with horizontal groove on hinge axis.
Anterior auricle may be slightly expanded at base	Anterior auricle may be slightly notched at base

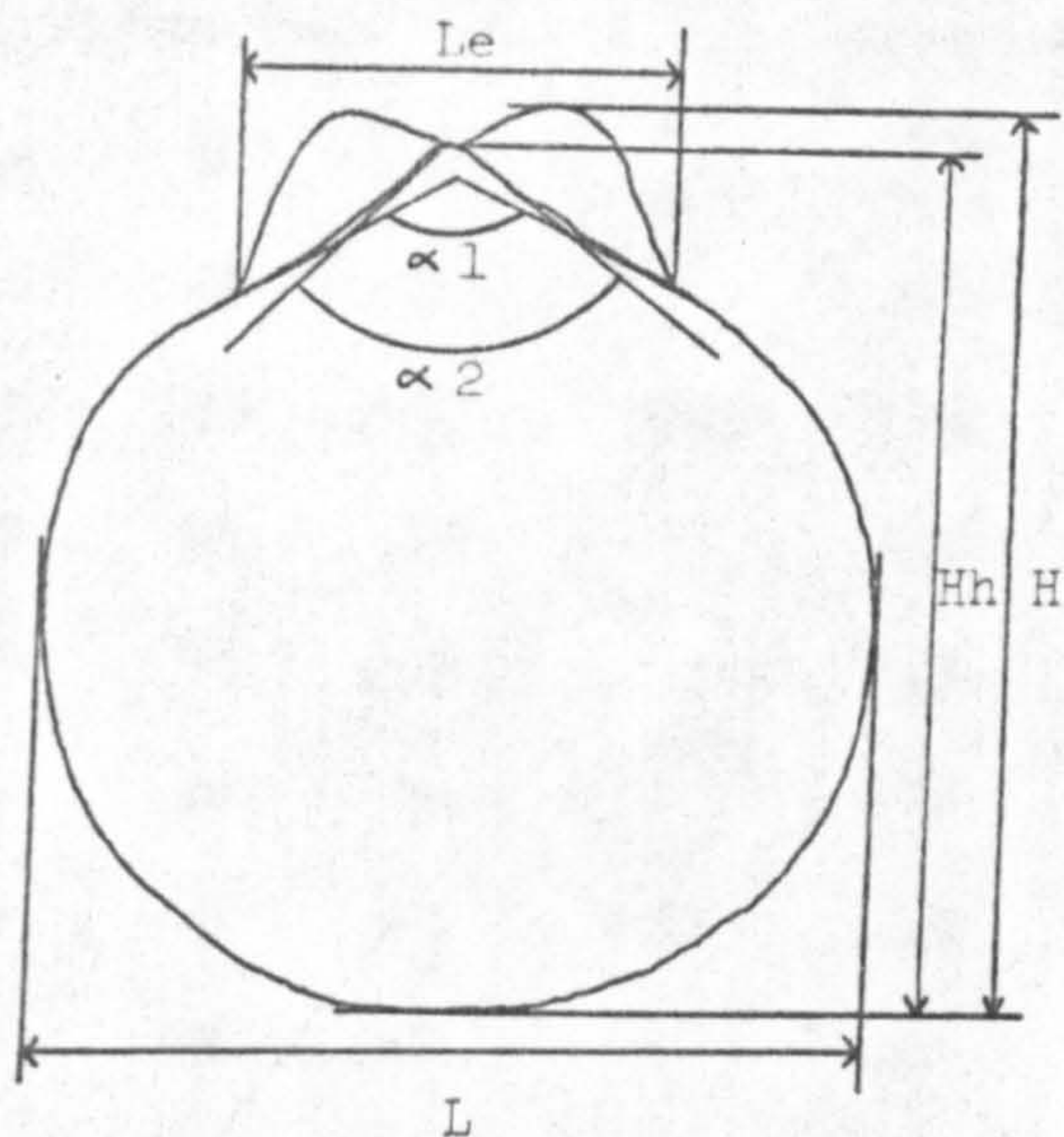


Figure 3.3.

Dimensions in Entolium.

Key:

L Length

Le Length of ears

H Height

Hh Height of hinge

Ha Hinge axis

Bn Byssal notch

Aac Anterior auricular crura

Pac Posterior auricular crura

R Resiliifer

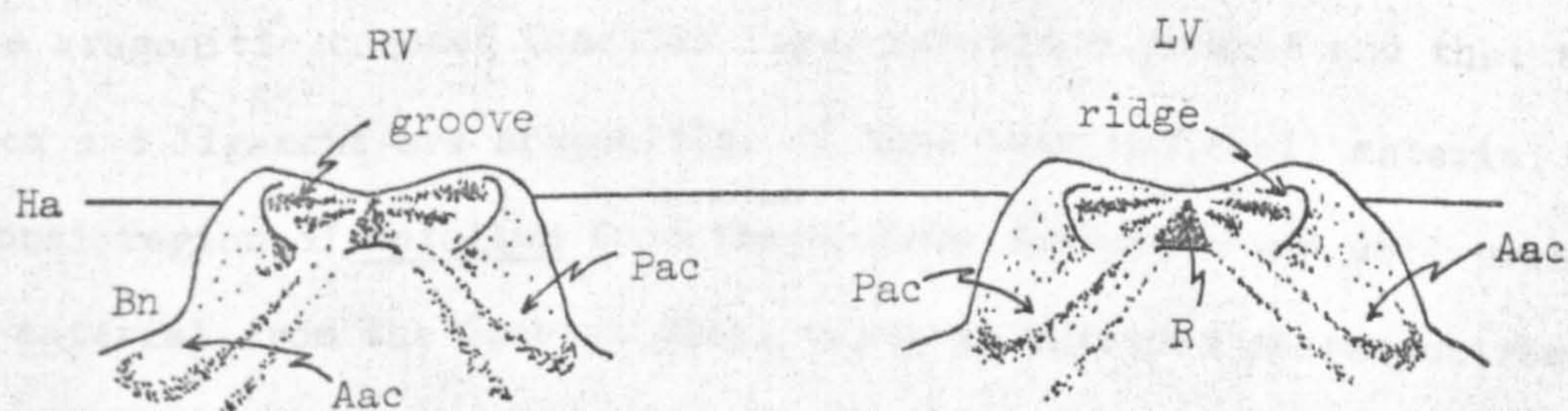


Figure 3.4.

Internal features of the hinge in Entolium.

Key as in Figure 3.3

Measurements. (see text figure 3.3)

	L	Le	H	Hh	α 1 min	α 2 max	B
SRAK IG.694	23	10	26	25	-	110	-
704	35	15	36	35	110	120	4'
1787	41	17	41	40	-	120	4'
2501	47	23	50	48	-	125	-
2511	46	19	49	47	-	120	-
2527	41	19	43	41	110	115	4'
2541	47	19	49	47	-	125	-
2548	40	15b	42	41	110	120	4
IGS R27/06	54	22	57	55	-	125	-

Discussion. The preservation of the Spilsby Sandstone fauna sheds further light on the shell structure of Entolium. The calcitic shell of Entolium is occasionally preserved in the centre of calcareous concretions in the Spilsby Sandstone. However close examination of the interior of the shell of such specimens (pl. 3 figs. 7 and 8) shows that the resiliifer is not preserved. Silicone rubber casts of the valve interiors taken from natural moulds whose shell is totally dissolved, show that the resiliifer is actually present. It is believed that the resiliifer was originally aragonitic and has been preferentially dissolved. Kennedy et al. (1969 p. 511) state that in the pectinacea there is an inner and outer calcitic foliated layer with a middle aragonitic crossed lamellar layer sometimes present and that the myostraca and ligament are aragonitic. I have examined shell material from the umbonal region of Entolium from the Spilsby Sandstone and well preserved similar material from the Speeton Clay, using an infrared photospectrometer. The Spilsby Sandstone specimens show calcite only while the Speeton Clay

material shows both calcite and aragonite present. The aragonitic myostracal region in Entolium probably accounts for the fragile umbonal region which is frequently the first part of the shell to become damaged by perforation. (pl. 3 figs. 1, 5, 9b).

Dhondt (1971) has given a thorough systematic review of E. orbiculare from the European Lower Cretaceous. The earliest specimens, that she records as Berriasian from the Spilsby Sandstone of Nettleton, are in fact of Upper Volgian age as there is no Upper Spilsby Sandstone north of Tealby. The synonymy list given here for the species is essentially supplementary to that of Dhondt and is compiled principally from the literature of Greenland and Russia. The discussion below is necessarily selective.

J. Sowerby (1817, p. 193), in the original description of E. orbiculare, clearly stated that one valve is smooth and the other concentrically striated. This appears to have been overlooked by many subsequent workers as recently as Turbina (1962) and Zakharov (1966). It is possible to find specimens of the right valve without the characteristic commarginal grooves, or with them only developed very close to the umbo. But it is the presence of these grooves in only some examples of the species from any single horizon which is regarded here as sufficient to characterise the species.

The most commonly used name for true E. orbiculare in Russia is E. nummularis (Fischer 1843). The types of the species came from Kursk and Khoroschovo. Fischer figured a smooth, probably left valve, but he also stated that the valves were ornamented by concentric grooves. He referred in the synonymy of the species to Pecten sp. Phillips

(1829, p. 8, pl. V, fig.11) from the Oxford Clay of Yorkshire. Phillips, later (1875, p. 326) named this specimen Pecten cingulatus. The specimen is a completely smooth valve and no entoliids with distinctive commarginal ornament have been found in the Oxford Clay. However some authors, eg. d'Orbigny (1945), attributed authorship of nummularis to Phillips.

The earliest records of "E. numulare" as such are from the base of the Upper Volgian of the Russian Platform (Gerasimov 1955, 1969), the Upper Volgian of the Russian Platform (Gerasimov 1955, 1969), the Upper Kimmeridgian of the North Urals (Zakharov 1974) and the Lower Kimmeridgian of Siberia (Zakharov 1966).

Fiebelkorn (1893) described a concentrically grooved Entolium from the 'Sand., braungrauer Kalk mit grossen Planulaten' - Kimmeridgian of north Germany as P. erraticus. The specimen that he figured is 23mm long and 26mm high with about 26 grooves. Gerasimov (1955) used E. erraticum for concentrically grooved entoliids thicker shelled than E. nummularis and with slightly wider umbonal angles - $112 - 113^\circ$ as opposed to $90 - 98^\circ$. Measurements on the umbonal angles of Spilsby Sandstone specimens range from a minimum of 95° to a maximum of 125° and the angle gradually increases with the age of the individual. The thinner shells recognised in E. nummularis may be due to aragonite dissolution as explained above. P. (E.) gothicus Krause (1908), also from the German Kimmeridgian, appears to be identical to Fiebelkorn's species and both are referred to E. orbiculare together with P. germanicus Wollema (1900) from the Neocomian of north Germany, and E. rossicum Glazunova (1960) from the Valanginian of the R. Rolya, north Siberia.

Smooth valves of Entolium from the later Jurassic and Lower

Cretaceous are commonly identified as E. demissum (Phillips. 1829) of which the holotype came from the Kellaways rock of Yorkshire. Left valves of E. orbiculare in isolation from grooved right valves are indistinguishable from E. demissum. In England the latest E. demissum assemblage occurs in the Shotover Grit Sands of Oxfordshire (SRAK & OUM). However the earliest grooved right valves (i.e. E. orbiculare) are shown by specimens in the IGS (Y. 1624, 1625) labelled 'Canal Pit, Swindon' and are associated with Exogyra virgula (Defrance) from the Kimmeridge Clay. Entolium recorded by Oates from the Hartwell Clay (1974), Middle Volgian has not yet been identified. Therefore there appears to be overlap of E. demissum and E. orbiculare, but the range of the overlap is not established. E. orbiculare continues into the Cenomanian and Turonian (Dhondt 1971) and is replaced by E. membranaceum Nilsson.

In North America Entolium irenense (McLearn, 1933) (?=pE. utukokense Imlay 1961) from the Albian/Aptian of Alberta and Alaska together with entoliids described by Crickmay (1930) from the late Jurassic/Lower Cretaceous of British Columbia, all lack the regular commarginal grooves and are thus differentiated from E. orbiculare.

Entolium nudus (Buvignier) as interpreted by Deschaseux (1936) from the Kimmeridgian-Portlandian of the Meuse/Haute Marne districts appears to be Camptonectes and not Entolium. It has distinctly unequal ears.

Occurrence. Kimmeridgian to Cenomanian of England; Kimmeridgian to Turonian of northern Europe; Middle Volgian to Albian of East Greenland; Upper Volgian to Valanginian of the Russian Platform; Kimmeridgian to Ryazanian of the north Urals; Kimmeridgian to Hauterivian of northern

Siberia.

Family PECTINIDAE Rafinesque, 1815
Genus CAMPTONECTES Agassiz in Meek, 1864

Camptonectes (Camptonectes) morini (de Loriol) 1867

Plate 5, figures 1-5, 7-9, Plate 6, figures 2, 3, 5.

- 1845 Pecten lens J. Sowerby; d'Orbigny, p. 476, pl. 42, figs. 1, 2.
- 1866 Pecten Morini de Loriol; Pellat, p. 207.
- *.1867 Pecten Morini sp. nov. de Loriol, pp. 107-108, pl. 10, fig. 6.
- .1880 Pecten Morini de Loriol; Blake, p. 234, pl. 10, fig. 3.
- 1936 Pecten morini de Loriol; Deschaseaux, p. 37.
- .1936 Camptonectes morini de Loriol; Spath, pp. 105-106, pl. 41,
figs. 5, 6.
- .1936 Camptonectes suprajurensis (Buvignier); Spath, p. 106, pl. 41,
fig.s 2-4, pl. 42, fig. 9.

Type Material. The original figured specimen is labelled 'Portlandien Moyen' of Boulogne. De Loriol Collection (untraced, ?Brussels)

Diagnosis. Adult shell small to medium size. Commarginal ornament normally absent. Radial ornament with density of c15 ribs per 10mm. Dorsal margins of flank usually punctate.

Material. Common in the sandy facies of the Spilsby Sandstone and Sandringham Sands, but also occurring less commonly in other facies of these formations. Middle Volgian to Ryazanian.

Description. Adult shell of small to medium size. Outline subcircular with projecting auricles. Left valve moderately inflated, right valve

only weakly inflated. Beak and umbo coincident, not projecting above the straight hinge line. In the left valve, the anterior auricle is larger than posterior auricle, and is not sharply delineated from the flank. Radial elements of the flank ornament pass onto the auricle and are traversed there by commarginal lamellae giving a reticulate pattern. The posterior auricle is small and separated from the flank by a groove. It is ornamented only by ribs and punctate grooves. In the right valve the anterior auricle is again much larger than the posterior. It is subtrapezoidal in outline, overhanging the byssal notch and distinctly separated from the flank by a groove. There is weak radial ornament overwhelmed by commarginal lamellae which drop vertically from the hinge line and as they swing towards the posterior die down into weak growth lines. The resulting pattern divides the ear diagonally into a lamellose and non lamellose regions. The posterior ear is similar to that on the left valve. The dorsal margins of the flank adjacent to the auricles are straight except for the anterior side of the right valve which is weakly concave and bears minute teeth forming the ctenolium. Because of the concave margin the umbonal angle increases with age from about 90° in juveniles to about 120° in adults. The ventral half of the shell margin is evenly rounded. The flank is ornamented by increasingly divergent fine radial grooves which maintain a density in the adult shell of about 15 ribs in 10mm. Branching takes place principally along the mesial line of the shell but is also present less commonly elsewhere on the flank. The centre and dorsal parts of the flank may appear smooth and ungrooved; this may be a feature of wear. The grooves in the dorsolateral parts of the flank are commonly punctate.

Internally the shell is smooth with a recessed triangular resilifer.

The shell is thickened around the byssal notch. In the right valve there appears to be at least 1 horizontal pair of teeth and grooves along the hinge axis. On the left valves this region is obscure due to preservation. Aragonitic shell in the ligamental and myostracal regions of the shell may be preferentially dissolved as in Entolium.

Measurements.

	L	Lh	Lha	H	B	α_1	α_2
IG.578	24	12	8	26	-	-	100
579	-	-	10	33	3'	-	-
662	18	9	7	20	5'	-	100
692	18	10	7	19	2'	95	105
1739	24	13	9	26	-	90	95
1760	20	9	5	22	5'	-	105
2099	23	-	-	23	3'	90	100
2100	32	14	9	-	7'	100	110

Discussion. Although P. Morini was first identified in the faunal lists of Pellat (1866), de Lorient did not formally describe and figure the species until the following year. The species was subsequently recognised by Blake (1880) from the Shotover Grit Sands of Swindon (Lower Volgian), and was discussed by Deschaseaux (1936) from the Paris Basin. Spath (1936) figured specimens from the Middle Volgian of East Greenland. He identified the less inflated valves with concave anterodorsal margins (i.e. right valves) as C. suprajurensis (Buvignier) and the more inflated and equilateral valves (i.e. left) as C. morini. I have examined further material from the same strata and they are undoubtedly one species. A specimen which appears to be C. morini was also figured by d'Orbigny (1845)

from the grès ferrifères de Koroschovo'. Subsequent figured material from the Russian Platform fails to confirm the existence of C. morini, and Gerasimov (1955) places d'Orbigny's specimen in synonymy with C. zonarius (see below).

Upper Jurassic camptonectids are in need of serious revision, although European Lower Cretaceous species have been reduced to a manageable number by Dhondt (1972). The following is a list of species comparable to C. morini together with their distinctive features and ages:

C. buchi (Roemer 1939) from the Oxfordian of North Germany has very closely set commarginal ornament.

C. lens (J. Sowerby 1818) From the Oxfordian of Oxford is generally more finely grooved and with more prominent punctations.

C. virdunensis (Buvignier 1852) from the Oxfordian of the Meuse is a short species with a narrower umbonal angle.

C. suprajurensis (Buvignier 1843) from the Kimmeridgian and Portlandian of the Ardennes is ornamented by very fine radial grooves and strong commarginal lamellae.

C. zonarius (Eichwald 1866) from the Volgian to Ryazanian of the Russian Platform is ornamented by paired commarginal lamellae which fuse together forming a tube.

C. striatopunctatus Roemer 1839) from the Neocomian of northern Germany has fine closely set commarginal ornament subordinate to the radial grooves which are punctate.

Occurrence. Lower Volgian to Middle Volgian of the Anglo-Paris basin; Middle Volgian to Ryazanian of eastern England and East Greenland and

?Volgian of the Russian Platform.

Subgenus

BOREIONECTES Zakharov, 1965

Zakharov (1965) introduced Boreionectes for large camptonectids from the Upper Jurassic and Lower Cretaceous with Pecten cinctus J. Sowerby (1822) as type species. In North America the large genus Mclearnia Crickmay (1930) is recognised in the Lower Cretaceous. General features of Mclearnia indicate relationships with the camptonectids, although Hertlein (in Moore Ed. 1969) places ?Mclearnia as group uncertain within the family Pectinacea.

I have examined casts of the type specimens of M. mclearnia Crickmay (1930b) through the courtesy of Dr. J. A. Jeletzky. The holotype (GSC 9701) shows parts of the interior and part of the external mould of a weakly inflated right valve. Further flank areas are visible on an incomplete specimen on the same slab. A paratype (GSC 9688) shows parts of the interior of a weakly inflated left valve. From these specimens I have not been able to find any features that would separate generically or subgenerically Boreionectes and Mclearnia, except that radial ornament is not visible on Mclearnia. Specimens of Boreionectes in the author's collection from the Lower Cretaceous of eastern England indicate that the radial ornament may be absent on some examples. Crickmay (1930, p.45) states In Mclearnia that 'When split the shell shows traces of fine, radial ribbing'. Without making further examination of specimens of Mclearnia, I am not yet prepared to refer all described boreionectids to that genus.

An American camptonectid referable to Mclearnia is Camptonectes

dettermani Imlay (1961), from the Albian of Alaska. This species was excluded by Zakharov (1965, p. 72) from Boreionectes. I have examined the holotype of the species through the courtesy of Dr. E. Kauffman (USNM). This together with paratype figures and also some figures of Entolium utukokense Imlay (1961, pl. 11, figs 2, 4, 6, 8 only) including the holotype appear to be one species, which shows moderately smooth shell ornament without radial grooves.

Camptonectes (Boreionectes) cinctus (J. Sowerby) 1822.

Plate 5, figures 6, 10-14, plate 6, figures 1, 4, 6, 7, plate 7 figures 1a,b.

- *v.1822 Pecten cinctus sp. nov. J. Sowerby, p. 96, pl. 371
- .1839 Pecten crassitesta sp. nov. Roemer, p. 27
- .1841 Pecten cinctus J. Sowerby; Roemer, p. 50.
- .1846 Pecten imperialis sp. nov. Keyserling, p. 295, pl. 15, figs 1-3.
- .1847 Pecten crassitesta Roemer; d'Orbigny, p. 584, pl. 430, figs 1-3.
- .1867 Pecten cinctus Sowerby; Judd, p. 250-251.
- v.1902 Pecten (Camptonectes) cinctus (J. Sowerby); Woods, pp. 152-156,
pl. 28, figs. 1-3, text fig. 2.
- .1960a Chlamys (Camptonectes) cf. imperialis (Keyserling); Glazunova,
p. 146, pl. 35, fig. 1.
- .1965 Camptonectes (Boreionectes) imperialis imperialis (Keyserling);
Zakharov, pp. 75-77, pl. VI.
- .1965 Camptonectes (Boreionectes) imperialis asiatica ssp. nov,
Zakharov, pp. 77-79, pl. 3, fig. 1, pl. 4, fig. 1,
pl. 5, fig. 1.
- .1966 Camptonectes (Boreionectes) imperialis (Keyserling), Zakharov,
pp. 52-53.

.1966 Camptonectes (Boreionectes) imperialis asiaticus Zakharov;

Zakharov, pp. 53-55, pl. 8, fig. 6, pl. 9, figs.

2-4, pl. 10, fig. 1, pl. 11, fig. 1, pl. 12, figs.

1,2.

.1972 Camptonectes (Boreionectes) cinctus (J. Sowerby); Dhondt,

pp. 34-40, pl. 1, fig. cl.

Types. J. Sowerby (1822) listed two syntypes which are preserved in BMNH, both numbered 43.300. His figured specimen came from the neighbourhood of Horncastle, Lincs, while the second specimen came from the alluvial clay of Suffolk. Although stated by Sowerby to be from the Inferior Oolite, their preservation in limonite oolite indicates that the Claxby Ironstone is a more likely source. The Horncastle specimen is here designated Lectotype.

Diagnosis. Adult shell large, outline subcircular with long auricles. Right valve moderately inflate; left valve moderately to weakly inflated and always less than left valve.

Material. 15 specimens. Occasionally found in the Lower Spilsby Sandstone (SRAK), Upper Spilsby Sandstone (SRAK, IGS) and in the upper part of the Mintlyn Beds (IGS): Upper Volgian to Ryazanian. Also abundant in the Claxby Ironstone, Lower Tealby Clay and Tealby Limestone, and occasionally in the Speeton Clay (Valanginian to Hauterivian).

Description. Specimens of Valanginian and Hauterivian age are used in this description to supplement information from the Spilsby fauna.

Adult shell large. Outline discoidal, with projecting auricles. Inequivalve. Left valve moderately inflated, right valve moderately to weakly inflated, but always less than the left valve. Valves subequilateral. Although the height/length ratio remains at about 1.0 throughout life (seen

in specimens of 50mm onwards), the umbonal angle gradually increases with size of shell. To show the growth change in single individuals, it is necessary to compare umbonal angle with distance from the umbo. The umbonal angle is measured between the tangents of pairs of points on the anterodorsal and posterodorsal flank margins equidistant from the umbo as shown in figure 3.6. The results are shown in Figure 3.5. The umbonal angle commences at $100-110^{\circ}$ and rapidly increases to about 130° by 30mm from the umbo. After 40mm the umbonal angle stabilises at about $140-150^{\circ}$ and may even decrease slightly. The levelling off of the umbonal angle suggests maturity of the individual. The increasing umbonal angle would allow water to be expelled from the dorsal margins of the shell more parallel to the dorsoventral axis than in juveniles which is a feature of free swimming pectinids (Stanley 1970).

In the right valve the ornament is composed of regular grooves 3-8mm apart, sometimes showing traces of raised fragile lamellae. Diverging fine radial grooves may be visible. Auricles large and elongate with raised commarginal lamellae and fine radial grooves. The posterior auricle is separated from the flank by a groove. In the anterior auricle the groove is weak or absent. In the right valve, the normal ornament is fine diverging radial grooves. However these may become corroded in older specimens. Commarginal ornament of growth halts with fragile raised lamellae may be present or absent or exist together in different parts of the valve. The auricles are subequal in overall length, but the anterior is recognised by a distinct byssal notch. Ornament on posterior auricle is composed of commarginal lamellae and radial grooves which may become obscure in older specimens. On the anterior auricle the commarginal lamellae are strong and irregular with little trace of radial ornament.

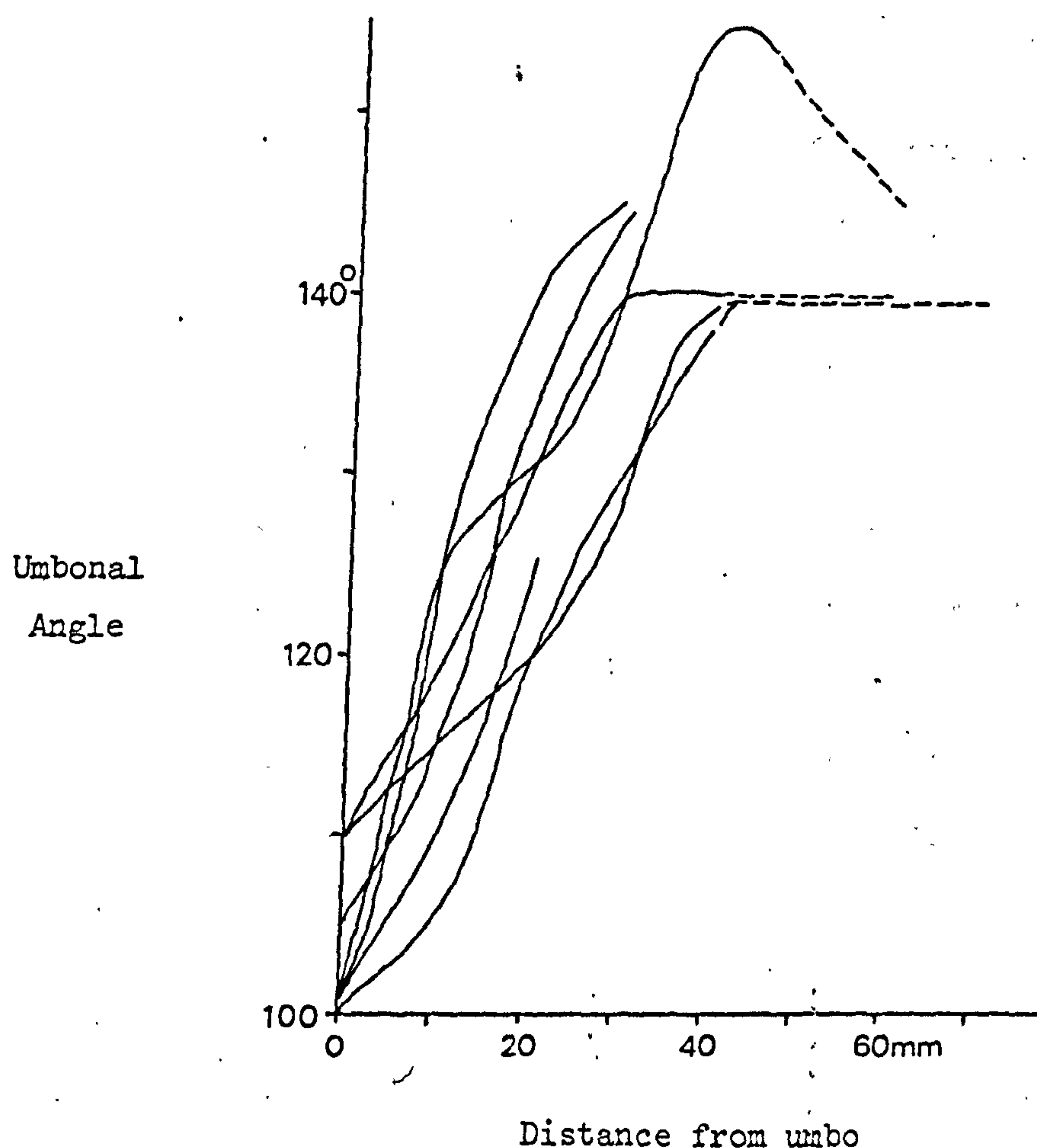


Figure 3.5.

Comparison of the umbonal angle of Camptonectes (Boreionectes) with distance along dorsal margin away from umbo. Solid line indicates presence of ctenolial spines in byssal notch. Dashed line indicates absence of ctenolial spines in byssal notch.

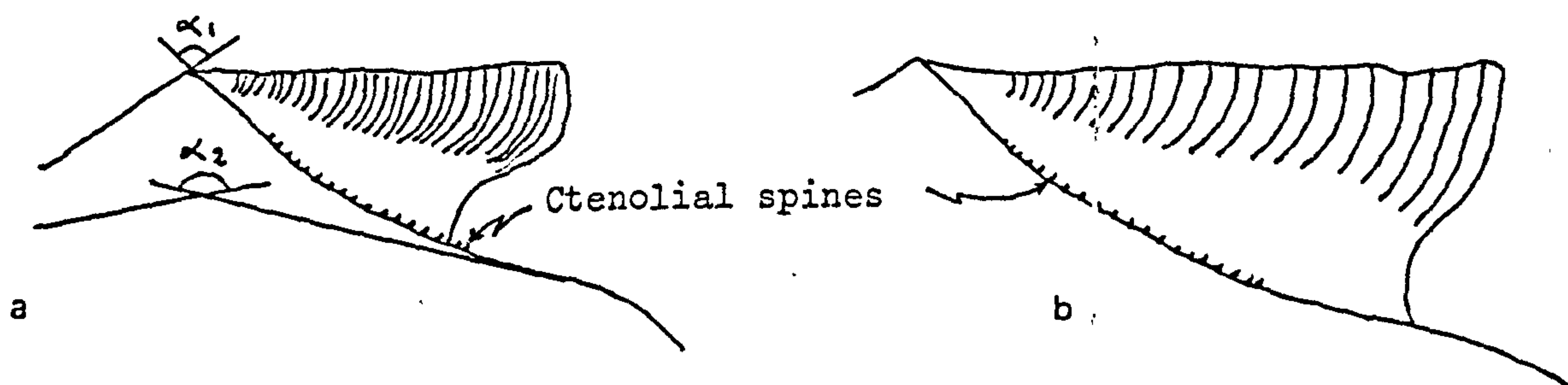


Figure 3.6.

The development of the ctenolium with age in C. (Boreionectes). Fig. 3.6a shows the position of measurement for the minimum and maximum umbonal angle and the ctenolium spines existing in the byssal notch. Fig. 3.6b shows older specimen with ctenolial spines not reaching the byssal notch.

The ctenolium persists usually to about 40mm from the umbo at which stage the shell is approximately 120mm in diameter. Above 120mm the ctenolium disappears and the relative size of the byssal notch decreases. This together with the change in the umbonal angle suggest that the animal was normally byssate up to 120mm and then became free-living with shell modified for free swimming. At 120mm the shell is thin being 3-4mm thick. Shells of larger diameter may locally reach 15mm thick suggesting that in old age individuals may settle to a sedentary existence and are commonly heavily encrusted with epibionts. The thickness of the shell would be a simpler form of defence than escape from predators.

Internally the shell is smooth. The large posterior adductor scar is deeply set together with the pallial line which is commarginal with a distinct sinus near the byssal notch. The resilifer is deeply set and in the right valve is flanked by two chevron shaped blunt teeth which correspond to poorly developed sockets in the left valve. Whether lateral ligament exists along the dorsal margin of the ears is not certain. (See Zakharov 1975, pl. 5 for very clear figure).

Measurements.

	L	Lh	Lha	H	B	α_1	α_2
SRAK IG.1807	44	-	-	47	7'	-	120
JG.421	-	90	48	110	12'	95	120
IGS TNN.255	123	101	51	129	46	105	130

Discussion. Although the type specimens of most species of Boreionectes are accessible for study, the range of variation in each species is far from established. The principal features for determining species are the inflation of the valves and the shape and size of the auricles.

The syntypes of C. (B.) cinctus are poorly preserved specimens. Workers rely on the figures of Woods (1902) for identification of the British species, and these figures do not adequately illustrate the range in variation. The shell of this species ranges from almost equivalve to almost plano-convex. The umbonal angle generally increases with age, and the ears may vary from 0.5-0.8 times the length of the shell. Without this knowledge subsequent species of Boreionectes from the Lower Cretaceous have been created on a limited range of features not realised as already present on C. (B.) cinctus.

It is clear that P. crassitesta Roemer (1839) from the Neocomian of north Germany belongs in synonymy with C. (B.) cinctus as Roemer himself admitted in a subsequent publication (1841).

P. imperialis Keyserling (1846) is more difficult to compare. 4 syntypes came from the Upper Valanginian on the R. Ishma, and one specimen was subsequently figured by Zakharov (1965, pl. 6) and declared the holotype (in fact the Lectotype). Zakharov differentiated C. (B.) imperialis from C. (B.) cinctus by its long cardinal margin with auricles of almost equal length, by the junction between the anterior auticle of the left valve and the flank being smooth (i.e. not grooved) and by the prominence of the umbo in the left valve. However the full range in morphology of C. (B.) cinctus from the Valanginian to Barremian of eastern England has never been illustrated and from specimens in the BMNH, SMC and SRAK collections it is clear that the above mentioned distinguishing features of C. (B.) imperialis are all found in C. (B.) cinctus. Furthermore the subspecies C. (B.) imperialis asiatica Zakharov (1965) was distinguished from C. (B.) imperialis imperialis by its larger apical

angle $c132^\circ$; the latter species has an apical angle of less than 120° . English material shows a range of $100-155^\circ$. It therefore seems likely that the subspecies of C. (B.) imperialis also belong in synonymy with C. (B.) cinctus.

C. (B.) cinctus differs from the preceeding species C. (B.) breviauris Zakharov (1965, type from the Middle Volgian of Siberia and C. (B.) praecinctus (Spath, 1936), type from the Middle Volgian of East Greenland, both of which have shorter and lower auricles. The full range in morphology of these species is not known and they may represent synonyms.

Subgenus. CAMPTOCHLAMYS Arkell, 1930.

Camptonectes (Camptochlamys) cf. intertextus (Roemer) 1839

Plate 1, figures 18a-c, 19, 20.

1839 Pecten intertextus sp. nov. Roemer, p. 27, pl. 18, fig. 23.

Material. 9 specimens (SRAK), basal Spilsby nodule bed, Middle Volgian, Nettleton, Lincs.

Description. The specimens are poorly preserved phosphatised internal and external moulds. Shell small to medium in size, relatively deep and short, weakly inaequilateral. Valves practically planoconvex. Left valve occasionally extremely weakly inflated. Right valve only weakly to moderately inflated. Umbo of left valve only moderately inflated. Umbonal angle angle $c80^\circ$. Auricles appear to be deep but can only be seen clearly on IG.1600. External ornament of fine straight radial riblets alternating one strong and one weak. These are crossed by relatively fine concentric raised lamellae, giving reticulate pattern which is reflected

on the interior of the shell. Auriculae crurae are absent or only very weakly developed.

Discussion. Several camptochlamids have been described from the northwest European late Jurassic. Pecten intertextus Roemer (1839) from the Oxfordian of north Germany is one of the most commonly used names. P. collineus Buvignier (1843) and P. Michaelensis Buvignier (1852) from the Oxfordian of the Ardennes and the Meuse respectively are almost certainly synonyms. Subsequently Cotteau (1855), with a brief but inadequate diagnosis, erected P. Portlandicus that de Loriol (1868) was the first to figure and describe accurately from the 'zone à Pinna suprajurensis, Portlandien' of the Yonne. In the meantime Contejean (1860) described P. Benedicti from the region of Montbeliard. All these species appear similar to the basal Spilsby specimens, but whether they are identical to one another remains to be established. The use of Roemer's name for this species is provisional.

Distribution. P. (C.) intertextus Roemer ranges from the Oxfordian probably as high as the Portlandian of northwest Europe.

Family BUCHIIDAE Cox, 1953

Genus BUCHIA Rouillier, 1845

Buchia rugosa (Fischer) 1837

Plate 8, figures 1a, b.

.1837 Inoceramus rugosus Bronn; Fischer de Waldheim, p. 175, pl. 46, fig.2.

?1846 Aucella Pallasii var. polita Keyserling, pp. 299-300, pl. 16, fig. 7.

.1888 Aucella Pallasii var. plicata Lahusen, pp. 9-11, pl. 1, figs.

21-24.

.1904 Aucella Pallasii Keyserling; Madsen, pp. 178-179, pl. 6, fig. 7.

- .1907 Aucella rugosa Fischer de Waldheim; Pavlow, pp. 182-186, pl. 1, figs. 6, 7.
- p.1908 Aucella Pallasii Keyserling; Sokolov. pp. 12-13, pl. 1, figs. 19, 20 only.
- .1911 Aucella mosquensis von Buch; Ravn pp. 457-458, pl. 22, fig. 6.
- .1936 Buchia rugosa (Fischer); Spath, p. 100, pl. 42, fig. 2.
- .1955 Aucella rugosa (Fischer de Waldheim); Gerasimov, pp 92-93, pl. 12, figs
- .1955 Aucella rugosa (Fischer); Imlay, p. 84, pl. 9, figs 20-27.
- .1959 Aucella rugosa (Fischer); Imlay, p. 157, pl. 16, figs. 18,19, 22-25.
- .1965 Buchia mosquensis (Buch) var. rugosa Fischer; Jeletsky, p. 19, pl. 2, fig. 1.

Types. The original material figured by Fischer de Waldheim came from near the Yaouza and the Moskwa rivers; it is untraced.

Diagnosis. Adult shell small. Left valve strongly inflated. Beak overhanging and recurved. Right valve almost flat with byssus ear almost in plane of commissure. Ornament of coarse regular commarginal folds.

Material. 2 specimens (SRAK), Basal Spilsby nodule bed, Middle Volgian, Nettleton, Lincs.

Description. Adult shell small and inflated. Umbo broad and projecting in the right valve, with small pointed, recurved and overhanging beak, which is weakly prosogyrate. The flank is distinctly twisted towards the posterior and is ornamented by low coarse commarginal folds. The diminutive right valve is weakly inflated and suboval in outline. The

ornament is as on the left valve. The byssus ear lies almost in the plane of the commissure.

Measurements.

	L	Lp	H	Hh	B
IG.1382	20+	14+	21+	14+	13

Discussion. B. rugosa is recognised here as a morphospecies within the broadly defined "biospecies" B. mosquensis (Buch) sensu lato. The latter species gives its name to the Buchia assemblage of 'Upper Kimmeridgian-Portlandian ss.' (Jeletzky 1965) which is widespread in the Arctic and North Pacific Realm (see fig. 5.6.). B. mosquensis s.s. is distinguished from B. rugosa by having lower ornament and more recurved shape.

The contemporary assemblage in the Indo-Pacific is B. blanfordiana which differs from B. rugosa by its larger adult size, more recurved shape and very depressed umbo.

Spath (1936) figured B. rugosa in association with B. mosquensis in the Middle Volgian of Milne Land, East Greenland. Also the figures of Madsen (1904) and Ravn (1911) indicate that the B. mosquensis assemblage is present in South Jameson Land.

In England buchiids are scarce. One specimen (Cunnington Collection, BMNH 24808) from the Upper Kimmeridge Clay near Devizes, Wilts., may be transitional to the preceeding B. concentrica (J. Sowerby) assemblage as there are weak traces of radial ornament. Other material from the Portland Sands of Wiltshire was described by Cox (1929) as B. mosquensis, but the ribbing is too fine and regular and probably represents B. fischeriana (d'Orbigny).

French Buchia have been described by Dutertre (1927) from the Boulonnais. From the Upper part of the Argiles de Châtillon (Kimmeridgian) he figured B. pellati (Pavlow), which although probably an element of the B. mosquensis assemblage, has a much lower and broader umbo than B. rugosa. From the Rochette nodule bed (Lower Volgian) he figured two specimens labelled Aucella bononiensis Paclow and A. mosquensis von Buch, but both appear to belong the former species and have a relatively more prominent umbo than B. rugosa, but these also probably belong in the B. mosquensis assemblage.

The buchiids figured by Lewinski (1923-24) from the Middle Volgian of Poland are all more elongate than B. rugosa and correspond to more typical B. mosquensis.

On the Russian Platform B. rugosa is restricted together with B. mosquensis to the D. panderi Zone (Lower part of the Middle Volgian). It is recorded widely elsewhere in Russia (See figure 5.6).

Occurrence. B. rugosa ss. is recorded from the Middle Volgian of eastern England, East Greenland, north west Canada, the Russian Platform, the North Urals and eastern USSR.

Buchia volgensis (Lahusen) 1888

Plate 8, figures 2-6.

*.1888 Aucella volgensis Lahusen, p. 38, pl. 3, figs 1-17.

v.1896 Aucella volgensis Lahusen; Pavlow, p. 549, pl. 27, fig. 1.

v.1896 Aucella volgensis Lahusen var. radiolata Pavlow, p. 550,
pl. 27, fig. 2.

- v.1899 Aucella volgensis Lahusen; Woods, pp. 69-70, pl. 10,
figs 1,2.
- .1907 Aucella volgensis Lahusen; Pavlow, pl. 2, fig. 10.
- 1964 Buchia volgensis Lahusen; Jeletzky, p.36, pl. 4, figs. 5-7.
- ?1965 Buchia volgensis Lahusen; Jeletzky, pl. 10, figs 4,5.
- .1969 Aucella volgensis Lahusen; Gerasimov, pl. 7, fig. 15.
- .1971 Aucella volgensis Lahusen; Pojarisskaja, pl.23, pl.30, fig. 2.

Types. Lahusen (1888) figured 17 syntypes from Kaschpur, Simbirsk; Starajn, Ryazan; C. nodiger Zone, U. Volgian, R. Olenek; and Manguyschlak. They appear to be untraced. Pojarisskaja (1971) designated as lectotype the original of Pavlow (1907), pl. 2, fig. 10) from the C. spasskensis Zone of Ryazan. Although this specimen may be a topotype, it may not have been a syntype. (It is in the Moscow University Museum.)

Diagnosis. Adult shell large. Left valve moderately inflated with prominent narrow umbo. Beak weakly recurved. Right valve weakly inflated. Byssus ear at high angle to commissural plane.

Material. 5 specimens (BMNH and SMC) believed by Casey (1973) to belong to the Upper Spilsby Sandstone, Ryazanian, from Donnington, Lincs.

Description. Adult shell large. Largest specimen is over 70mm from the umbo (broken) to the distal part of the commissure. In the left valve the umbo is narrow and projecting with a weakly recurved slightly prosogyrate beak. The flank is moderately inflated and twisted towards the posterior. The ornament is only seen reflected on the internal moulds. It appears to be regular weak commarginal folds which are finer in the more juvenile stages. The right valve is very weakly inflated with a low almost

rectangular umbo. The ornament is similar to that on the left valve, but radial ribs are weakly seen especially on pl. 8 figs 3,4. The byssus ear is at a high angle to the plane of commissure.

Measurements

Left valves		L	Lp	H	Hh	B
SMC	B11337	50	c42	c62	52	20'
	11338	45	38	49	43	17'
BMNH	*81069	59	-	65+	63	19'
	*81075	31	23	40	-	12'
Right vales						
SMC	B.11337	48	38	52	49	10'
	11338	41	37	40	39	8'
	11339	19	c16	20	19	4'
	*81069	53	45	60	58	16'
	*81075	34	26	44	36	16'

* measurements from photographs.

Discussion. Buchia volgensis was first recognised in the Spilsby Sandstone by Pavlow (1896) from specimens in the SMC collection bearing the label Inoceramus imbricatus Bean MS. He based a new variety, var. radiolata upon one specimen (B.11338) which shows distinct but fine radial ornament. This ornamentation can be made out on most of the other specimens. Pavlow states that he had seen specimens of B. volgensis from North Germany. The specimens together with others identified as Aucella Keyserlingii Lahusen and A. terebratuloides Lahusen occurred in the Lower Cretaceous of Salzgitter and also in the Claxby Ironstone of Lincolnshire. All these

latter specimens belong to a variable species, B. lamplughi (Pavlow 1907), typical of the Hauterivian in north west Europe.

The Spilsby Sandstone specimens correspond closely to the type figures of Lahusen (1888). The specimen subsequently designated lectotype by Pojarisskaja (1971) is rather smaller than the types and has more regular ornament. She also records the species from the Valanginian of the Russian Platform.

B. volgensis is widespread in the Boreal Realm exclusive of the north Pacific and is recognised as a distinct assemblage by Jeletzky (1965) in the Upper part of the Ryazanian. Jeletzky's figures (1964, 1965) of B. volgensis from the Upper Ryazanian of the Richardson Mountains, northern Canada, are similar to the Russian syntypes, but are generally much smoother in the left valves and with a less inflated posterior margin. Also the right valves are more oval and the umbones less projecting than in the syntypes or the Spilsby specimens. Buchia aff. volgensis (Lahusen) (Jeletzky, 1964, p. 30, pl. 1, figs 9-11) from the Ryazanian of Yukon and British Columbia represents an assemblage of late Ryazanian age intermediate between B. volgensis ss. and the early Valanginian B. keyserlingii assemblage (Jeletzky, 1971, 1973.)

Spath (1947) discussed and figured B. volgensis from the Muslingeelv Member, South Jameson Land, East Greenland, however this material belongs to the B. okensis (Pavlow 1907) assemblage (see Jeletzky, 1968, p. 6) and is of Ryazanian age (H. kochi Zone). Subsequently B. volgensis was recognised by Spath (1952) in association with Praetollia maynci from the Wollaston Forland, but this was reidentified by Jeletzky (1973, p.52) as B. terebratuloides s.l. and believed to be late Jurassic. Surlyk (1973)

however has shown that P. maynci and H. kochi have almost identical stratigraphic ranges and are of Ryazanian age. A true B. volgensis assemblage has not yet been recognised in East Greenland.

Occurrence. Widespread in the upper part of the Ryazanian in eastern England, northern Canada, the Russian Platform, the Urals and northern Siberia; also extending into the Valanginian of the Russian Platform.

Order	TRIGONOIDA Dall, 1869
Superfamily	TRIGONIACEA Lamarck, 1819
Family	TRIGONIIDAE Lamarck, 1819
Genus	IOTRIGONIA Van Hoepen, 1929

Discussion. The genus is characterised by having an elongate shell, with smooth posterior area, obsolete carinae and chevron shaped ribs on the flank. The type species, I. crassitesta Van Hoepen (1929 OD), comes from the upper part of the Lower Cretaceous of Southern Africa. Although regarded by Cox (in Moore Ed. 1969) as an Austral genus, it has been recorded by Saveliev (1958) in Mangyukschlak and by Gerasimov (1969) from the Russian Platform. In addition material that has been referred to Trigonia herberti Munier-Chalmas and the type figure of Trigonia incurva Bennet, from the Anglo-Paris basin, are here referred to Iotrigonia. These species are the earliest recorded Iotrigonia and are of Middle Volgian age. They do differ from the genotype by having myophorellid type flank ornament, but having examined the variation in other trigoniids, I believe it reasonable to group these forms together because of the distinctive inflated, divided and smooth posterior in mature individuals.

The origins of Iotrigonia are obscure. Van Hopen (1929) originally

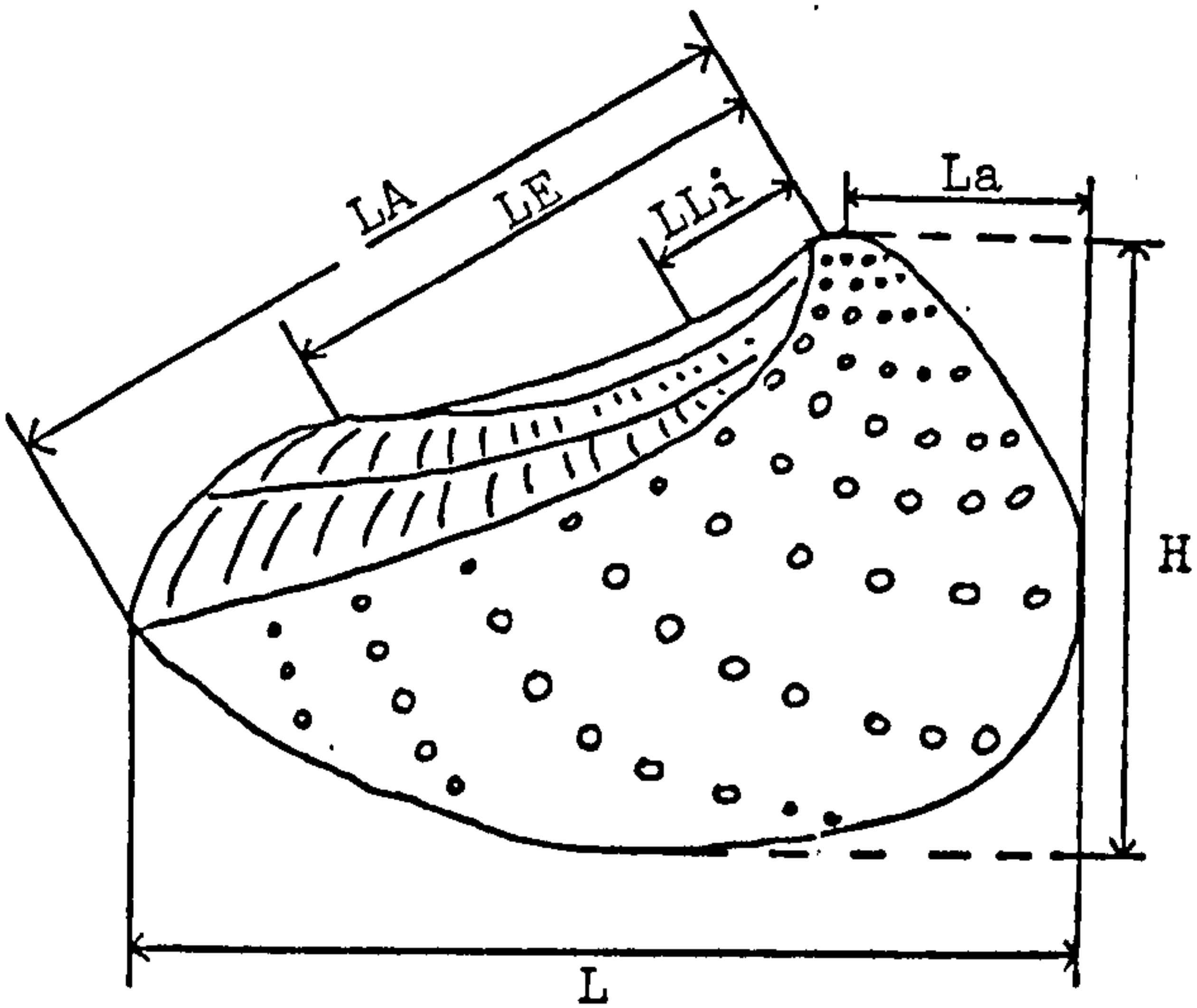


Figure 3.7a

Dimensions in Trigonoida

Key:

- | | | | |
|----|-----------------------|-----|--------------------|
| L | Length | LLi | Length of ligament |
| La | Length anterior | LLu | Length of lunule |
| Lp | Length posterior | H | Height |
| LA | Length posterior area | B | Breadth |
| LE | Length of escutcheon | | |

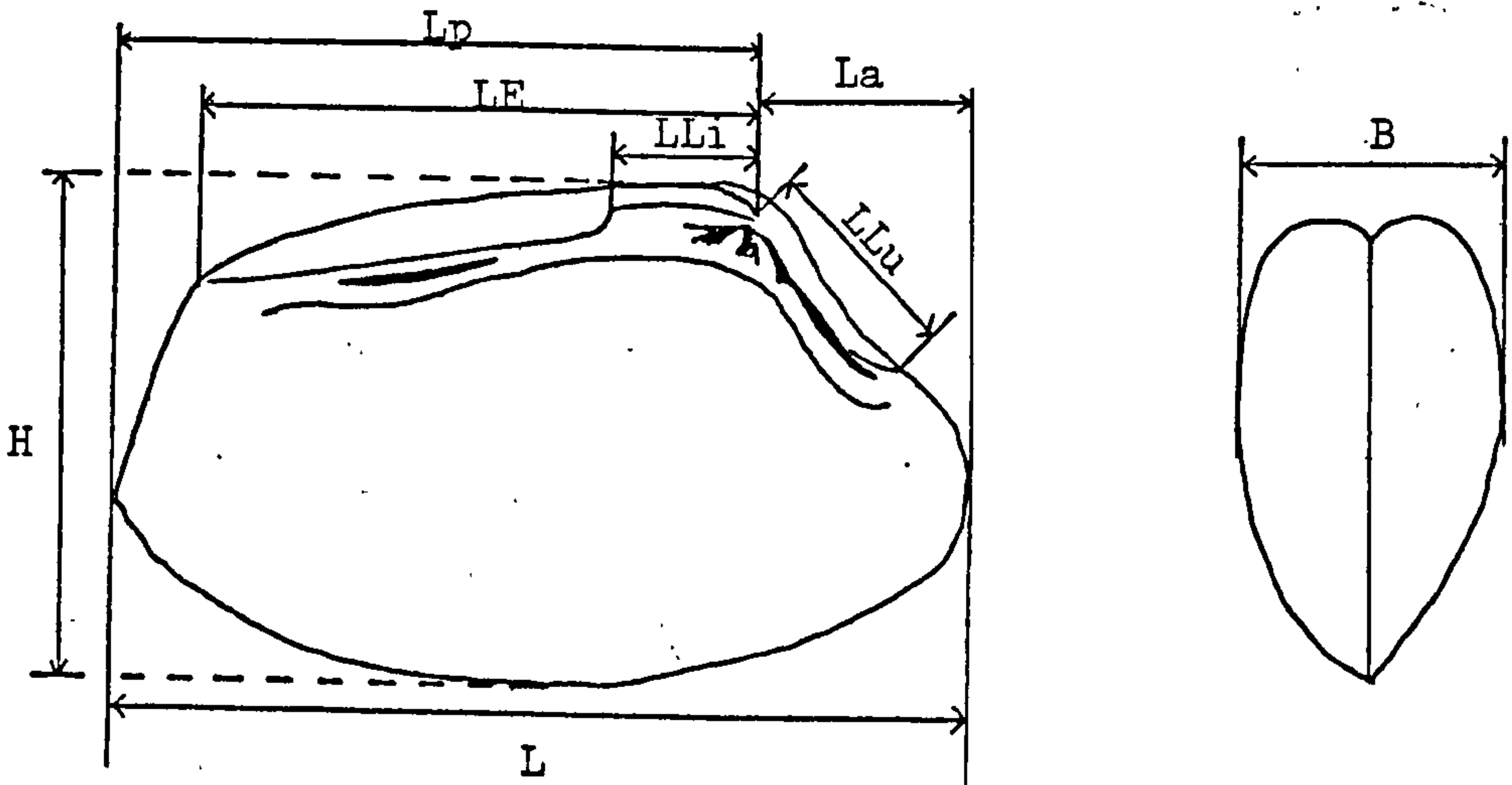


Figure 3.7b

Dimensions in Heterodonta and Myoida.

Key: as in Figure 3.7a.

placed it as a subgenus of Megatrigenia. In the adult stages this would not appear tenable, but Rennie (1936, p. 340) believed that an association is recognisable in the neanic ornament. Saveliev (1958) suggested that Iotrigenia is derived from the Jurassic Vaughonia at the beginning of the Cretaceous. Vaughonia has a myophorellid-type posterior area with chevron shaped rows of flank tubercles. I think that it is likely that Iotrigenia has evolved from Myophorella either directly or via Vaughonia, and that Megatrigenia may have subsequently arisen from Iotrigenia. However this needs further study, especially on well preserved neanic ornament.

Iotrigenia atlantica sp. nov.

Plate 13, figures 1a, b, 3.

?1865 Trigenia Heberti sp. nov. Munier Chalmas pp. 416-417, pl. 4, fig.5.

p?1872 Trigenia incurva Bennet; Lycett, p. 42 (unlabelled figure only).

Types. Holotype: SRAK JG. 1668, basal conglomerate of the Muslingeelv Member of the Hesteelv Formation, H. kochi Zone, Ryazanian, Locality 308 (Spath 1947), 3km. south of Crinoidbjerg, South Jameson Land East Greenland. 10 Paratypes: 9 specimens (SRAK), information as for holotype, 1 specimen (IGS CE1554) from the Lower Mintlyn Beds, H. kochi Zone, Ryazanian, Flood Relief Channel 400 yds. west of Abbey Station, West Dereham, Norfolk.

Diagnosis. Adult shell of medium size, low and recurved. Flank ornamented by myophorellid-type rows of tubercles. Posterior area smooth and inflated.

Description. Adult shell of medium size, up to 65 mm in length and strongly inequilateral. Commisural outline slightly tapered to posterior and recurved. Umbo prominent, with anterior margin distinctly inflated curving gently into the slightly curved ventral margin. Posterodorsal margin concave.

Flank ornament. of coarse rows of blunt tubercles which are separated by broad grooves and which drop vertically from the posterior carinal area and swing gently forward as they approach the ventral margin. Near the anterior the rows of tubercles tend to break up into an irregular finer ornament. The posterior area is strongly inflated, with a particularly prominent ventral half separated from the more diminutive dorsal part by the mid area groove. There are no carinae or tuberculation and the whole surface is smooth except for growth lines. The escutcheon and other features cannot be seen clearly on the specimens.

Measurements. (see Figure 3.7).

	L	H	B	LA	LE
SRAK JG. 1668	65	42	17'	55	32
IGS CE1554	51	32	c13'	-	-

Discussion. I. atlantica is based on specimens from the Ryazanian of eastern England and East Greenland. Other specimens occur in the erratic blocks of Norfolk associated with ammonites of the P. oppressus and S. preplicomphalus Zones; one is figured here as I. cf. atlantica as it is not sufficiently well preserved to allow close comparison.

T. heberti Munier Chalmas (1865) (non Deslongchamps; see Cox 1952, p. 55) from the Portlandian of northern France differs from I. atlantica only in the less prominent inflation of the posterior area and the more tapered outline. The type figure of Trigonia incurva Bennet (1831) differs from I. atlantica principally in the greater shell depth, but the specimen, believed to be in the collection of the Academy of Natural Sciences, Philadelphia has not yet been traced: it could be gerontic. The name Trigonia incurva has subsequently been used widely, but for elongate

myophorellids which belong to M. portlandica (Cox 1925) or close allies.

Trigonia Falcki Rouillier and Vossinsky (1849) from the Upper Volgian and Ryazanian of the Russian Platform, is not well figured. The type figures show a deep form which lacks detail of the posterior area. Gerasimov (1969) placed it in Iotrigonia and in one of his figures (pl. 8, fig. 5) the typical smooth divided and inflated posterior area can be seen. In other figures (pl. 8, figs 1-4) he shows specimens preserved as composite moulds with chevron shaped ribbing on the flank which is reminiscent of Vaughonia. I. falcki therefore appears to be a deep form somewhat similar to I. incurva. Precise comparison with I. atlantica must await clear illustration of Russian Platform material.

I. scapha (Agassiz 1840) occurs in the Upper Claxby Ironstone (Upper Valanginian/Hauterivian) of Lincolnshire and is widespread in Europe (Gillet, 1964). The species differs from I. atlantica by being less elongate and recurved, and possessing chevron shaped ribs or rows of tubercles on the flank.

Occurrence. Although the species is only definitely recorded from the Ryazanian of eastern England and East Greenland, it may also occur in the Middle and Upper Volgian of eastern England and in the Portlandian of northern France.

Genus

LAEVITRIGONIA Lebkuchner, 1932

Discussion. The known range of Laevitrigonia (Laevitrigonia) can be extended into the Cretaceous as the genus occurs commonly in the Cinder Bed horizon of the Vale of Wardour, Wiltshire, and in the Whitchurch Sands

of Buckinghamshire which Casey (1963) regards as of Ryazanian age.

Laevitrigonina (Laevitrigonina) manseli (Lycett) 1874

Plate 9 figure 1.

*v.1874 Trigonina Manseli sp. nov. Lycett, pp. 86-88, pl. 19, figs. 3,4.

c.1929 Trigonina gibbosa J. Sowerby var. manseli Lycett; Cox, pp. 159-160

v.1964 Laevitrigonina gibbosa (J. Sowerby); Casey and Bristow, p. 125.

Discussion. One specimen (IGS CE.3752) is preserved as a mould in a small waterworn pebble of medium to fine grained glauconitic sandstone, with no associated macrofauna. The pebble was found with other erratic boulders at Leziate, Norfolk. Casey and Bristow (1964) referred this enigmatic specimen to L. gibbosa, but it bears tuberculation oblique to the growth lines and therefore corresponds to L. manseli, known from the Portland beds of the Anglo-Paris basin.

Laevitrigonina (Laevitrigonina) wightensis (Strand) 1928.

Plate 9, figure 2.

v.1875 Trigonina Michelotti de Lorient var.; Lycett, pp. 92-93,
pl. 20, fig. 7.

*.1928 Trigonina wightensis sp. nov. Strand, p. 71.

v.1929 Trigonina wightensis Strand; Cox, pp. 160-161, pl. 3, fig. 1.

Discussion. One specimen (SMC B.85668) is labelled Lower Greensand, Pottton, Bedfordshire. It is preserved as calcitic shell with some buff limestone matrix infilling the umbo. It presumably came from the basal conglomerate of the Lower Greensand and represents part of the fauna reworked from earlier deposits. L. wightensis has been discussed by

Cox (1929). Although recorded from the Portland and Purbeck Beds, the species is most abundant in the Swindon Roach of the Lower Purbeck beds (SRAK Coll.). The most likely source for the Potton specimen would have been from the eroded Purbeck Beds of the margins of the London-Midlands platform. L. damoniana (de Loriol 1867), which is the typical Portland Beds Laevitrignia, is distinguished by its finer ornamentation.

Genus

MYOPHORELLA Bayle, 1878

Myophorella (Myophorella) intermedia (Fahrenkohl) 1844.

Plate 9, figures 3a-c, 4a,b; plate 5 figures 1a-c, 2; plate 11, figures 1a-c, 2a-c, plate 12, figures 1,2.

- *.1844 Lyriodon intermedium sp. nov. Fahrenkohl, p. 796, pl. 19, fig. 2.
- ?1845 Trigonia clavellata Parkinson; d'Orbigny, p. 460.
- ?1849 Trigonia janoi sp. nov. Rouillier & Vossinsky, pp. 349-350,
pl. K, fig. 80.
- .1867 Trigonia intermedia Fahrenkohl; Eichwald, p. 601.
- .1869 Trigonia intermedia Fahrenkohl; Eichwald, pl. 23, fig. 6.
- v.pl872 Trigonia ingens sp. nov. Lycett; pp. 24-25, pl. 8, figs. 1-3.
- v.1877 Trigonia exaltata sp. nov. Lycett, pp. 184-185, pl. 38, fig. 2.
- .1896 Trigonia intermedia Fahrenkohl; Stremoukhov, pp. 258-261,
pl. 7, fig. 6.
- 1900 Trigonia exaltata Lycett; Woods, p. 74.
- pl900 Trigonia ingens Lycett; Woods, p. 75.
- .1923 Trigonia Bronni var. intermedia (Fahrenkohl); Lewinski, p. 73,
pl. 13, fig. 2,3.
- .1936 Trigonia aff. thurmanni Contejean; Spath, p. 113, pl. 41,
fig. 8, pl. 42, fig. 10.

- .1936 Trigonia sp. Spath, pl. 41, fig. 7.
- .1955 Trigonia intermedia (Fahrenkohl); Gerasimov, pp. 52-53,
pl. 3, figs 1-3.
- .1969 Myophorella intermedia (Fahrenkohl); Gerasimov, p. 74, pl. 9,
fig. 3.

Types. The type material is described from 'An der Moskwa'.
Stremooukhov's (1869) revision of Upper Jurassic Russian trigonids failed to mention the existence of Fahrenkohl's original specimen(s). It will probably be necessary to designate a neotype and if possible this should be based on one of Stremooukhov's specimens which were stated to have been deposited in the Geological Museum of the University of Moscow.

Material. c140 specimens. Common in the sandy facies of the Lower Spilsby Sandstone, Roxham and Runcton Beds, P. oppressus to S. lamplughii Zones, Middle to Upper Volgian. (BMNH, IGS, SMC, SRAK)

Diagnosis. Adult shell of medium to large size. Flank ornament of rows of coarse tubercles, often becoming irregular near the anterior margin. Posterior area with low commarginal lamellae and irregular low meandriform swellings sometimes developed.

Description. Adult shell of medium to large size, thick, moderately inflated. Commissural outline subtrigonal to subquadrate. Strongly inequilateral. Anterior short with truncate margin. Ventral margin gently curved. Posteroventral junction slightly angled to rounded. Posterior margin weakly curved. Posterodorsal margin relatively straight in younger specimens up to c65mm length (Plate 11 fig. 3), thereafter becoming increasingly concave (Plate 10; fig. 1). The umbo is relatively narrow

and becomes increasingly prominent with age. The ornament of the flank is variable. The basic pattern in mature specimens is of slightly sigmoidal rows of coarse blunt tubercles which curve gently forward from the posterior carina and near the anterior margin are weakly recurved in a ventral direction (Plate 12, fig. 1); a final dorsal twist may be present on some rows of tubercles immediately before the anterior margin is reached (Plate 10, figure 1). The size of the tubercles is variable from very coarse in BMNH 49987 (type of T. exaltata) (Plate 10 figure 1) to relatively fine in IG.2499 (Plate 12, figure 1). Sometimes the anterior rows of tubercles break into an irregular pattern (IG. 2499).

The antecarinal region is very narrow. The posterior carina itself is very well marked in the juvenile stages where closely packed small tubercles are fused together in a carina (Plate 11, figure 3). In later stages the tubercles become coarser and progressively more isolated and even obsolete in some specimens (Plate 10, figure 1). The area is flat to very weakly inflated and relatively wide. In the juvenile stage it is ornamented by isolated raised lamellae which are commarginal and pass right across the whole area. The mid area groove cuts this ornament after about 5-10 mm from the umbo and thereafter the ornament is of a coarse growth line style. There is a row of fine tubercles defining the escutcheon carina, and also a row of tubercles on the ventral side of the mid area groove. In mature specimens these tubercles tend to be broad and low, irregular in shape and tending to fuse with irregular meandriform swellings that cross the whole posterior area (Plate 10, figure 1).

The escutcheon is smooth and concave, although some of the escutcheon carina tuberculation may overflow onto the ventral side. The

ligamental area extends a short distance along the escutcheon and there is a short but strong nymph. Internally the shell is smooth (Plate 9, figure 3c) with a strong trigoniid dentition. The posterior adductor and small pedal retractor scars are deeply set. There is a distinct projection on the posterior margin corresponding to the position of the mid area groove at the posterior margin.

Measurements.

		L	La	LA	LE	LLi	H	B
BMNH	49987	137	16	122	76	33	88	22
SRK	IG.2496	106	8	98	60	27	69	20
	2497	66	5	62	42	-	45	15
	2498	102	9	65	101	26	72	21
	2498	-	5	-	-	7	26	9
	2499	110	13	101	59	-	73	220

Discussion. Although M. intermedia (Fahrenkohl) is well known from the Russian Platform, the only clear figures of the species were by Stremoukhov (1896). English specimens of intermediate size, e.g. IG.2497 (pl. 11 fig. 2), correspond almost exactly to Stremoukhov's figures of the species. The medium sized shell is subquadrate in outline and has a very wide posterior area with an almost straight posterodorsal margin and slightly projecting escutcheon. The English example quoted above was found in the same slab as larger Myophorella that correspond to Lycett's (1872) description and figures of T. ingens, and clearly belongs to the same species group: hence T. ingens is placed in synonymy with M. intermedia. The three figured syntypes of T. ingens were stated by Lycett to be in the Lynn Museum. Woods (1900, p. 75) noted that they were lost and recent searches have failed to locate them. However one cast remains of Lycett's plate 8, figure 1, in the IGS (114232) Lycett's material came from the 'Neocomian formation'

(Presumably Sandringham Sands or an erratic block) of Downham, Norfolk. Some Claxby Ironstone myophorellids which Lycett (1877) figured subsequently as T. ingeus differ from the original specimens by having a smaller maximum size and distinctive lamellose and pustulose ornament over the whole posterior area. They are redescribed below and renamed M. (M.) claxbiensis sp. nov. Also in 1877 Lycett described T. exaltata (refigured here on pl. 10 fig. 1) from the Drift of Norfolk. The matrix is a moderately fine grained sandstone with moulds of Falcimytilus and lucinids which appears to be Spilsby Sandstone or Lower Sandringham Sands. The ornament is extremely coarse and some of the rows of tubercles are straight but others break into a more irregular pattern on the anteroventral region. Transitional examples to more typical M. intermedia are found in the Middle Volgian erratic blocks at Leziate, Norfolk.

Lewinski (1923) recorded M. intermedia as a variety of T. bronni from the Middle Volgian of Poland. The figured specimen was moderately deep and finely ornamented for the species. Spath (1936) figured large myophorellids from the Middle Volgian of East Greenland as T. aff. thurmanni Contjean and T. sp. These and specimens collected subsequently (IHGPC) from the same region all correspond closely to the Lower Spilsby Sandstone specimens.

M. intermedia is closely related to myophorellids that occur in the Kimmeridgian and Portlandian of the Anglo-Paris basin. Unfortunately these species are still not well defined and described. M. portlandensis Cox (1925) from the Portland Limestone, differs from M. intermedia by having more delicate flank ornament and being more elongate and less quadrate. M. swindonensis, from the Lower Volgian, is more elongate with a

narrower posterior area. M. suevica (Quenstedt) (= M. pellati Munier-Chalmas), also from the Lower Volgian is extremely elongate with an acute junction between the ventral and pallial borders.

In the Spilsby basin, the contemporary M. tealbyensis Lycett is smaller than M. intermedia with much finer flank ornamentation and tuberculation on the posterior area. M. keepingi from the Ryazanian is distinguished by lamellose tubercles on the posterior area.

From the Lower Volgian (here interpreted as Middle Volgian of the north Urals), Saveliev (1960) described a group of closely related species including M. uralica and M. borealis which have a comparatively more elongate shape than M. intermedia with more inflated anterior region. The flank ornamentation is very similar but the posterior area is narrower with a prominent mid area groove and weak tuberculation on the posterior carina, on the ventral margin of the mid area groove and on the escutcheon carina.

In the Ryazanian of the north Caucasus and Mangyukschlak respectively occur M. (M.) loewinsonlessingi (Renngarten 1926) and M. (M.) invitulana Saveliev (1958). These were originally described as Valanginian but the age has been revised by Louppov, Bogdanova and Lobatcheva (1975). Both these species have much more regular commarginal lamellae on the posterior area than M. intermedia, and there is no trace of tuberculation.

For suggested phylogenies of Boreal Myophorella around the Jurassic-Cretaceous boundary see discussion of M. tealbyensis and figure 3.8.

Occurrence. Middle to Upper Volgian of eastern England and the Russian Platform. Middle Volgian of East Greenland and Poland.

Myopherella (Myoporella) keepingi (Lycett) 1877.

Plate 12 figures 3, 4a-c; Plate 14, figures 1a-c, 2a-c, 3, 4, 5a-c, 6.

*v.1877 Trigonia Keepingi sp. nov. Lycett, p. 196, pl. 35, figs 1,2.

pl900 Trigonia ingens Lycett; Woods, p. 75.

Types. Lycett figured two syntypes, refigured here plate 14 figs. 1a-c, 2a-c (SMC B.11235 and 11236 respectively) labelled 'Middle Neocomian Acre House, Tealby, Lincs'. The preservation of the matrix of B. 11235 is a coarse grained calcite cemented glauconitic sandstone typical of the Spilsby Sandstone. SMC B. 11236 is here designated lectotype. (see also discussion below.

Diagnosis. Adult shell medium sized, trigonal in outline with concave posterodorsal margin. Posterior area tuberculate in juvenile stages becoming more lamellose in adults.

Material. c70 specimens. Rare in mid Spilsby nodule bed (SRAK). Common in Clay-Ironstone facies of the Mintlyn Beds (IGS). H.kochi - S. stenomphalus Zones, Ryazanian.

Description. Adult shell usually medium sized with maximum length c75 mm and moderately inflate. Commissural outline trigonal with truncate anterior having a rounded angle with the ventral margin. The posterodorsal margin is weakly concave and the shell tapers to a rounded posterior. The flank is ornamented by rows of coarse tubercles (c15 rows in a specimen about 65 mm long). The rows of tubercles leave the posterior carina perpendicularly and swing gently forward, sometimes dropping slightly to give a sigmoidal shape. The posterior carina is defined in the juvenile stage by fine

closely set tubercles. After 20 mm from the umbo these become larger and more isolated and transversely elongate. There is a narrow antecarinal space in some examples; in others it is absent. The posterior area is weakly inflated. In the juvenile part up to about 25 mm from the umbo the median groove is clear, but the rest of the surface is covered by fine regular rows of tubercles, the most prominent being those adjacent to the escutcheon and median groove. In the later formed part of the posterior area the tubercles become fused together to give irregular meandriiform lamellae which may pass right over the median groove from posterior to escutcheon carinae. The escutcheon is smooth and broad with some of the irregular escutcheon carina tubercles spreading onto its margin. The specimens are too incomplete for detailed measurements.

Discussion. Doubt exists concerning the horizon and locality of the types of T. keepingi. Lycett (1874, p. 197) states 'they were found in the vicinity of Tealby, in the bed of hard limestone which has also yielded T. Tealbyensis'. The only M. tealbyensis that I have seen in association with ammonites are restricted to the S. preplicomphalus Zone, Lower Spilsby Sandstone, of Southern Lincolnshire and in erratic blocks of the same age in Norfolk. I suspect that Lycett was referring to the Spilsby Sandstone as a whole and not to a particular bed and that the types of M. keepingi may have come from a higher horizon in the Spilsby Sandstone than M. tealbyensis and if so would be unlikely to have come from Acre House as the Upper Spilsby Sandstone is absent from Tealby northwards. I have never seen any Lower Spilsby Sandstone containing M. keepingi, and the restriction of in situ specimens to the Ryazanian of Lincolnshire and Norfolk would support an Upper Spilsby Sandstone horizon for the types.

Adult M. keepingi are generally smaller than M. intermedia and differ principally in the tuberculate and lamellose ornament of the posterior area. M. claxbiensis described below, is even smaller than keepingi, the outline is semicircular without distinct angulation at the anteroventral border and with a straight posterodorsal margin. For discussion of the origin of M. keepingi see discussion of M. tealbyensis.

Specimens of Myophorella in the authors collection from the H. kochi Zone of South Jameson Land, East Greenland have been examined closely but are not sufficiently well preserved to indicate that they belong to M. keepingi.

Occurrence. H. kochi to S. stenomphalus Zones of the Ryazanian of Eastern England.

Myophorella (Myophorella) claxbiensis sp. nov.

Plate 15, figures 1a, b, 2, 3a-c, 4a-c, 5a,b, 6a-c.

v.1877 Trigonia ingens sp. nov. Lycett, pl. 36, figs. 5,6.

.1879 Trigonia ingens Lycett, pp. 207-208.

p.1900 Trigonia ingens Lycett, Woods, p. 75.

.1912 Trigonia ingens Lycett; Wolleman, p. 162.

.1924 Trigonia ingens Lycett; Gillet, p. 80.

1965 Myophorella ingens (Lycett); Gillet, p. 400.

Types. Holotype, IGS 27040, From the Claxby Ironstone, Acre House Mine, Lincs. Paratypes: there are abundant paratypes from the Claxby Ironstone in the collections of the IGS, BMNH, SMC and SRAK. Material in the author's collection has only been found in the lower part of the Claxby

Ironstone and at Benniworth Haven has been found in association with Proleopoldia, a Valanginian ammonite. The Thurrell Collection in the IGS has 26 further paratypes found in association with Peregrinoceras albidum in the topmost beds of the Upper Spilsby Sandstone at Biscathorpe Wold Gravel Pit.

Diagnosis. Adult shell c60 mm in length. Outline semicircular. Flank ornament of slightly sigmoidal rows of tubercles. Posterior area weakly inflated and ornamented with coarse commarginal lamellae, occasionally giving way to finely tuberculate ornament.

Description. Adult of medium size and moderately inflated. Adult shell length normally about 60 mm. Commissural outline usually semicircular, with evenly rounded anterior and ventral margins. Posterior margin weakly inflated to obliquely truncate. Posterodorsal margin straight. Umbo is prominent but not projecting. In some specimens which are slightly more elongate, the anterior margin tends to be more truncate (Plate 15, figures 2, 4a). The flank ornament is composed of slightly sigmoidal rows of tubercles which vary from relatively coarse (Plate 15 figure 1) to relatively fine and delicate (Plate 15, figure 5a). The posterior carina is defined by a row of tubercles which are very small and closely spaced near the umbo and become progressively larger and more widely spaced towards the posterior border. The posterior area is relatively narrow. Near the umbo it tends to be flat or stepped at the mid area groove and becoming weakly inflated near the posterior. The ornament of the area is dominated by irregular raised commarginal lamellae (Plate 15, figures 4, 6b) but sometimes gives way to a more tuberculate ornament (Plate 15, figure 3c). Irregular lamellose tubercles mark the ventral margin of the

mid area groove and the marginal carina. The escutcheon is smooth and weakly concave. The internal features are typically trigoniid.

Measurements.

	L	La	LA	LE	LLi	H	B
SRAK KY.106	47	6	45	30	12	35	14'
761	61	4	59	40	17	40	14'
787	59	3	57	38	16	40	17'
1073	58	5	55	36	14	40	16'
1077	50	4	48	30	12	34	13'
AfBH uncat	75	5	73	64	-	50	-
IGS 27040 (Holotype)	56	7	52	35	11	38	14

Discussion. Lycett (1872) originally based T. ingens on specimens from the Sandringham Sands or Drift of Norfolk (see discussion of M. intermedia). Subsequently (1877) he figured further specimens from the Claxby Ironstone under the same name. Subsequent workers, principally Woods (1900), have used T. ingens widely for the Claxby Ironstone form without realising it was different species. As T. ingens is a junior subjective synonym of M. intermedia, the name must disappear and M. claxbiensis is here proposed for the Cretaceous species which occurs in the late Ryazanian and Valanginian of eastern England.

Wolleman (1912) recorded Trigonia ingens from the Valanginian Polyptychiten Schichten of West Germany. A slightly crushed composite mould is figured here from Lindhorst (Plate 15 figure 2), it shows relatively coarse rows of stout tubercles on the flank, but the posterior

area is less prominently ornamented than most Claxby Ironstone specimens, although this may be a preservational feature. Maas (1895, p.282, pl. 9, fig. 7) described Trigonia roelligiana from the Gault of Wilhelmshöhe as being very similar to T. ingens, but the comparison is doubtful as the figured specimen is very poorly preserved.

Litschkow (1912) labelled some figured specimens from the Neocomian of Manguyschlak T. ingens, however, despite a superficial resemblance to T. claxbiensis, Saveliev (1958) has shown that they belong to the Hauterivian T. litschkovi Mordvilko (1953) and possess distinctive v-shaped early growth ribs which place them within the genus Litschkovitrigonia Saveliev. Specimens from the Claxby Ironstone and topmost Spilsby Sandstone have roughly comarginal ribs in the early growth stages which are therefore distinct. Renngarten (1926) records Trigonia cf. ingens from the Hauterivian of the northern Caucasus, but this cannot be confirmed here.

Occurrence. Late Ryazanian to Valanginian of eastern England and in the Valanginian of northern West Germany.

Myophorella (Myophorella) tealbyensis (Lycett) 1875

Plate 13, figures 4a, b, 5a-d, 6, 7a-d.

*.1875 Trigonia Tealbyensis sp. nov. Lycett, p. 114.

v.1877 Trigonia Tealbyensis Lycett, pl. 28, fig. 7.

.1900 Trigonia tealbyensis Lycett; Woods, p. 79.

.1965 Myophorella tealbiensis (Lycett); Gillet, p. 400.

Type. Holotype: SMC B.11241, Spilsby Sandstone, unhorizoned, Tealby, Lincolnshire.

Diagnosis. Mature shell of medium size, subtrigonal in outline. Flank with c20-25 rows of fine tubercles. Mature ornament of posterior area composed of extremely fine regularly spaced tubercles.

Material. 45 specimens. Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, of south Lincolnshire (SRAK); Erratic blocks of the same horizon in Norfolk (IGS & SRAK); Reworked in the basal conglomerate of the Lower Greensand, Bedfordshire (SMC).

Description. Mature shell medium sized with maximum length 63 mm. Subtrigonal in outline and moderately inflated. Anterior margin evenly rounded onto gently curved ventral margin. Posterior obliquely truncate and posterodorsal margin approximately straight. Umbo prominent. Flank ornamented by 20-25 regular rows of close fine tubercles. The rows swing gently forward from the posterior carina. There is no trace of irregular ornament on the anterior of the shell. The antecarinal depression is very narrow. The posterior carina is marked by a row of tubercles which are very fine in the early stages and crowded tightly against one another becoming increasingly isolated with age. The posterior area is flat and moderately wide. There is a distinct mid area groove separating the area into a slightly smaller dorsal portion and a larger ventral part. In the juvenile stages straight commarginal lamellae pass across the whole posterior area. About 5mm from the beak the lamellae start to break up into radial rows of lamellar tubercles. On the escutcheon carina and the ventral margin of mid area groove the lamellar tubercles are particularly pronounced. The escutcheon is concave and smooth except for some lamellar tubercles which may spread over from the escutcheon carina (seen clearly on the holotype). The internal features are typically trigoniid.

Measurements.

	L	La	LA	LE	LLi	H	B
SRAK IG.2490	63	6	47	35	8	36	12'
IG.2493	38	4	35	24	7	27	9'

Discussion. The holotype of M. tealbyensis is incomplete lacking most of the posterior part of the shell. During this study, complete specimens have been prepared from natural moulds and are illustrated for the first time. Lycett's original description states that the holotype came from a bed of hard limestone of Neocomian age, which has been accepted by subsequent workers (eg. Gillet, 1965) and was suggestive of the Tealby Limestone. However the matrix is a coarse grained calcite cemented sandstone, typical of the Spilsby Sandstone. All the dateable specimens of M. tealbyensis are referable to the S. preplicomphalus Zone, and it is likely that all other ex situ specimens are of the same age.

There is only one species that appears to be closely related to M. tealbyensis. It was named T. densinoda Etheridge (1881) and was found in the Cinder Bed of the Vale of Wardour, Wilts and is therefore probably of Ryazanian age (Casey 1963). 2 syntypes are preserved in the IGS and the figured specimen (IGS 11900) is here designated lectotype. The species grows to a largersize than M. tealbyensis, the rows of tubercles are more numerous (45+) and the anterior is more truncate. M. densinoda has not been found in the Spilsby Basin, but may have inhabited a slightly less saline environment of a northerly draining system of the London-Midlands High.

The origin of M. tealbyensis may be associated with M. muricata

Goldfuss & Munster which comes from the Lusitanian of Portugal (see Choffat 1885) and which has regular forward swung rows of moderately fine tubercles. The form with which M. muricata is associated and with which it merges is the distinctly contrasting M. lusitanica (Sharpe) which has strongly recurved rows of variable sized tubercles. However the posterior areas of both M. muricata and lusitanica may bear tuberculate ornament which may pass right over the escutcheons and is shown more clearly than on the holotype of M. tealbyensis. It may eventually be possible to isolate the lineage of M. tealbyensis as a distinct subgenus but it is worth waiting to obtain more comparative data regarding the group.

The relationships between the species of Myophorella discussed here are not clearly understood. The ideas discussed briefly below are summarised in Figure 3.8. Saveliev (1960, p. 205) has already stated that the M. borealis/uralica group, present in the Lower Volgian (here interpreted as Middle Volgian) of the north Urals, may have given rise to M. ingens (Lycett) in the British Isles and to M. loewinsonlessingi Renngarten and M. invitulana Saveliev in the Caucasus and Manguyschlak. It is not clear whether Saveliev is referring to M. ingens (Lycett 1872, pl. 8, figs 1-3) interpreted here as M. intermedia (Fahrenkohl) of Middle to Upper Volgian age, or to M. ingens (Lycett 1877, pl. 36, figs. 5,6.) from the Valanginian and here renamed M. claxbiensis. It seems certain from the Spilsby Basin material that M. claxbiensis is clearly derived from M. keepingi in the Upper Ryazanian and they represent a single lineage. The problem of the origin of M. keepingi remains. It could have come from the Russian stock, but there are also other possibilities from within the Spilsby Basin. The basic flank ornament of M. keepingi is very similar to that of M. intermedia

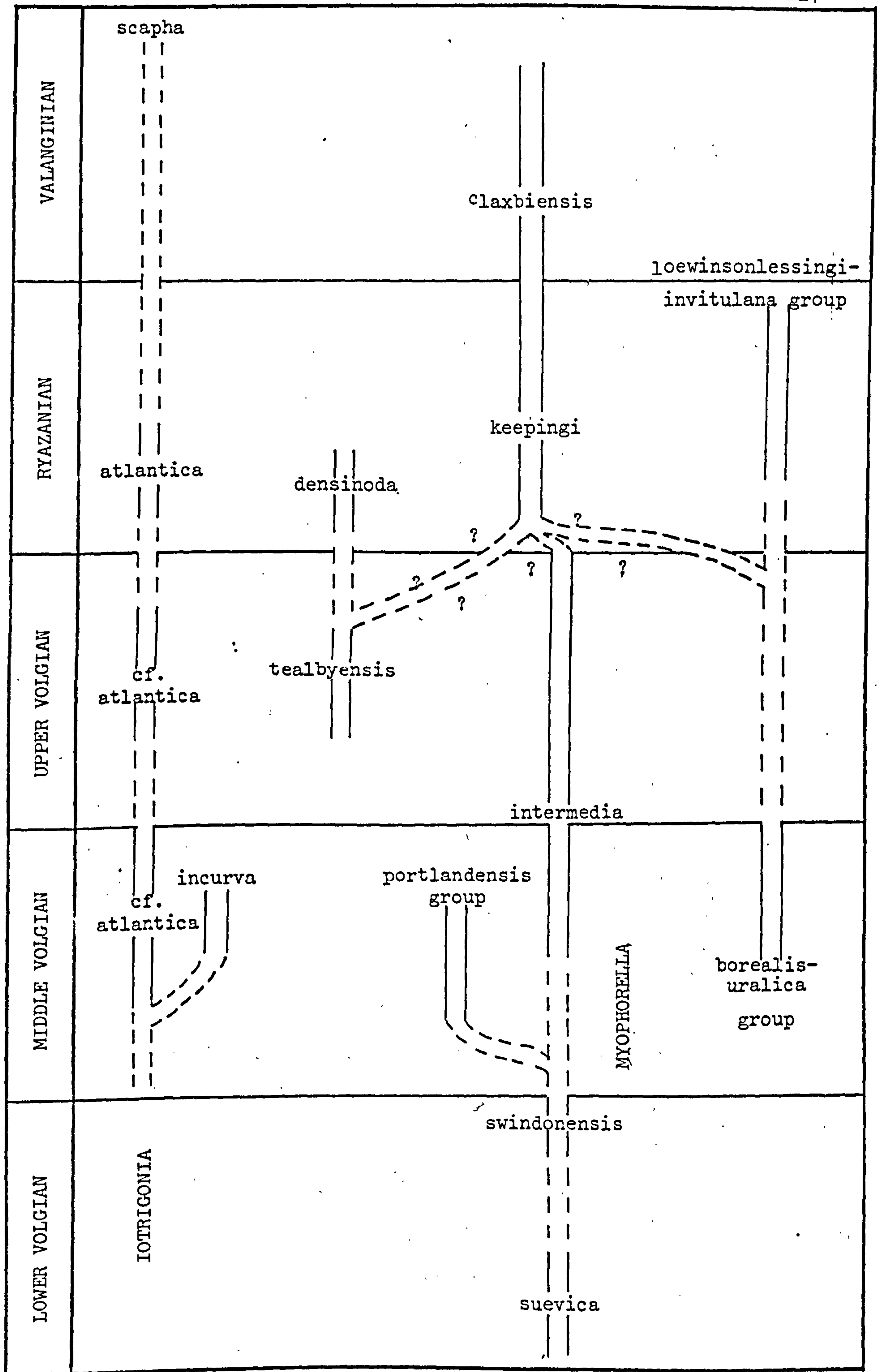


Figure 3.8

Suggested phylogenies for the Spilsby and associated trigoniids

while the posterior area ornament suggests affinity with M. tealbyensis.

There are therefore three possibilities for the origin of M. keepingi.

Detailed examination of myophorellid lineages in East Greenland and on the Russian Platform should help resolve the problem.

Occurrence. Restricted to the S. preplicomphalus Zone of the Upper Volgian of Eastern England.

Subclass	HETERODONTA Neumayr, 1884
Order	VENEROIDA Adams and Adams, 1856
Superfamily	LUCINACEA Fleming, 1828
Family	LUCINIDAE Fleming, 1828

Discussion. The family Lucinidae appears in the Palaeozoic and is well represented in the Mesozoic; however the relationships between the three subfamilies of Chavan (in Moore Ed. 1969) are not clear. Chavan differentiates the subfamilies on shell shape, ornament and relative size of the anterior adductor muscle scars. Unfortunately the range in variation of the groups is overlapping and there may be difficulty in allocating a genus to a subfamily.

Until Chavan (1937-38) published his first study on the classification of lucinids, 'Lucina' was almost the only generic name used. Since late last century a few generic names have appeared based on mesozoic species. Although these genera are moderately well described and illustrated, the inherent variability at generic level is not satisfactorily known. As far as possible I have used only generic names based on Mesozoic lucinids although one species is dubiously referred to a Tertiary form. The following is a list of Mesozoic genera which have non denticulate margins.

Capital letters denote anterior and posterior lateral teeth. Numerals represent cardinal teeth. The use of brackets denotes feeble development of a structure. Names are based on Chavan (1969) and supplemented by Wellnhofer (1964):

<u>Luciniola</u> Skeat & Madsen 1898	A	P	(3a)	2a	3b	4b
<u>Perampliata</u> Arkell 1936				2a	3b	
<u>Mesomiltha</u> Chavan 1938	(A)	(P)		2a	3b	4b
<u>Jagonoma</u> Chavan 1946	A	(P)	(3 ^a)	2a	3b	4b
<u>Mesolinga</u> Chavan 1951	A	P		2a	3b	4b
<u>Discomiltha</u> Chavan 1952				2a	3b	
<u>Discoloripes</u> Wellnhofer 1964	(A)	(P)	3a	2a	3b	4b

Although the subfamilies of Chavan are followed here for the sake of precedence, the divisions are not satisfactory. Much further work is necessary for revision even of the Mesozoic lucinids alone.

Genus CODAKIA Scopoli, 1777

Codakia? crassa (J. de C. Sowerby) 1827

Plate 16 figures 1, 2a,b, 3, 4, 5, 6.

*.pl827 Lucina crassa sp. nov. J. de C. Sowerby, p. 108, pl. 557,
fig. 3.

1867 Lucina crassa J. de C. Sowerby; Judd, p. 251.

1948 Lucina crassa J. de C. Sowerby; Cox and Arkell, p. 33.

Types. Sowerby (1827) records syntypes from near Horncastle, Lincs (of which a specimen was figured) and from Brambury Hill, Sutherland all of which are untraced. A neotype is designated here : IGS CE 3453, erratic

boulder of Lower Spilsby Sandstone/Sandringham Sands. The species is here restricted to the Upper Jurassic specimens and those from the Oxfordian of Scotland are excluded.

Diagnosis. Adult shell normally 20-23 mm in length, subcircular in outline. Exterior almost smooth with delicate commarginal growth lines and fine radial grooves.

Material. 14+ specimens (IGS & SRAK). All from erratic boulders of Lower Spilsby Sandstone/Sandringham Sands, some of which are in association with P. oppressus, Middle Volgian, Leziate, Norfolk.

Description. Adult shell of medium size, with length usually 20-23 mm. Shell subcircular and robust with low umbo and small sharp prosogyrate beak. Lunule obscure but appears narrow and shallow in right valve and deeper in left. Flank with undifferentiated posterior area almost smooth but ornamented by delicate growth lines and fine radial grooves. Internally the hinge line is well developed, the formula is as follows:

AII	0	AIV	(0)	2	0	4b	n	(PII)	(0)	(PIV)
		AIII	(0)	3a	0	3b	n		(PII)	

In the left valve, AII and AIV are short and bluntly laminar, bordering a short deep socket for AIII and all situated directly under the anterior end of the lunule. 2 is narrow, laminar and opisthocline with a weak socket in front and a well developed triangular socket behind. 4b laminar and opisthocline and close to ventral margin of the nymph which appears to be deeply set. Posterior end of hinge thickened but feeble traces of short PII and PIV with intervening socket can be seen. In the right valve, AIII is bluntly laminar and with an ill defined socket above. 3a is a small

laminar tooth running vertically below the umbo, but with dorsal end obscured by the lunule. Large triangular socket for 2. Tooth 3b is prominent, weakly opisthocline, narrowly tapered but triangular in posterior aspect. Large triangular socket for 4b bordering the elevated nymph. Posterior end of hinge thickened, but bearing minute PIII.

Shell interior may be smooth or pustulose. The margin is smooth and thickened below the pallial line. Ovate posterior adductor scar. Anterior scar elongate and close to pallial line, and only weakly impressed. Some specimens show a weak oblique median groove.

Measurements.

		L	H	B
Holotype:	IGS CE 3453	21	22	4'
	SRAK IG.622	20	21	6
	629	24	25	5'
	630	23	23	6
	1724	21	22	5

Discussion. Sowerby's original name has been rarely used in the past, although varieties are recorded (see Cox and Arkell, 1948 & Stoll, 1934). These varieties appear unrelated to C. crassa as interpreted here. The original description was brief; 'Nearly orbicular, convex; covered with thick slightly elevated, concentric laminae; superior margin obtuse; lunule linear, concealed; valves thick. A little wider than long, rather flat in the middle, and irregular; the beaks are very small. Found by Mr. Weir in Sandstone at Horncastle and By R.I. Murchison Esq. at Brambury Hill, Sutherland. Our figure is from a specimen from the former place.'

The figure is extremely close in profile to that of IG.629 (Plate 16

figure 2a, 2b) and the commarginal ornament identical. Sowerby could have overlooked the fine grooves. There is no reason to believe that the figured type came from an erratic block as suggested by Cox and Arkell (1948, p.33). Judd (1867) has stated that Sowerby's specimen came from the 'sandstone at Bolingbroke' from which Spilsby Sandstone fossils are well known.

Mesozoic lucinids with radial ornament are rare, and it is for this reason alone that L. crassa is provisionally placed in Codakia. Contjean (1860) described L. radiata from the Kimmeridgian of Montbeliard; this species shows similar radial ornament to L. crassa, but the umbo is broad and more projecting and the hinge is unknown. The only Spilsby species with which C? crassa can be confused is Discoloripes sp. nov? (Plate 18, figure 7, 12) which is distinguished by having a more depressed umbo, no radial ornament and an almost polished shell surface.

Occurrence. Middle Volgian of eastern England.

Subfamily MYRTEINAE Chavan, 1969

Genus MESOMILTHA Chavan, 1938

Mesomiltha? kostromensis (Gerasimov) 1955.

Plate 18, figures 1-6.

*1955 Loripes kostromensis sp. nov. Gerasimov, pp. 67-68, pl. 6, figs. 1-3.

1964 Loripes (Loripes) kostromensis (Gerasimov); Wellnhofer, pp. 79-81, pl. 7, figs. 14-23, text figs. 50a, 50b.

Types. Holotype: Gerasimov Collection, No. 984, Moscow University Museum, Lower Kimmeridgian, Polovchino, Kostromsk District. 22 paratypes exist from

the same area.

Diagnosis. Shells up to 12 mm length, elongate, suboval. Adults (c15mm) slightly more elevated. Surface ornament of regular commarginal raised lamellae.

Material. 70+ specimens (IGS and SRAK). Common in association with P. oppressus, in erratic blocks of Lower Spilsby Sandstone/Roxham Beds of Middle Volgian age, Leziate, Norfolk. Two specimens (SRAK) from the Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, south Lincs.

Description. Adult shell small, up to 18 mm in length. Moderately inflated. Juveniles elongately suboval. Depth increases with size. Posterodorsal margin is almost straight. Umbo low and mesial. Details of lunule and escutcheon obscure, but appear to be narrow. Surface ornament of regular commarginal lamellae about 1 mm apart in adult part of shell. The posterior area is poorly differentiated by weak increased flexure in ornament. Hinge and internal features are not seen.

Measurements.

	L	H	B
IG.446	18	16	8
527	14	13	3'
521	17	15	3'
1751	14	11	3'
2360	20	18	4'
3420	18	16	-

Discussion. The generic allocation of M. kostromensis is doubtful.

Both the type specimens, which Gerasimov referred to Loripes, and the English material discussed here, do not show the hinge. However, specimens figured by Wellnhofer (1964) do show a hinge which is very narrow. 3a and 3b are fine and recurved. 2 is straight and opisthocline. AI is the only clear lateral tooth. Superficially the hinge resembles Mesomiltha (Chavan, 1938) although the cardinal teeth have a different format of 2, 3b, 4b and it is in this genus that L. kostromensis is provisionally placed. Wellnhofer referred his specimens to Loripes (Loripes), but this a Tertiary and Recent genus with a short hinge line and robust teeth.

L. corbisoides d'Orbigny (1845) from 'grès chlorites de Saragula' differs by retaining the elongate suboval outline to a greater size (31 mm in figure). L. phillipsiana d'Orbigny (1845), from the 'grès chlorite, oxfordien, Saragula' and 'schistes de Makarief, R. Unja' is distinguished by a sharply delineated posterior area causing a short, sharply truncate posterior margin. In both these species, the hinge line is unknown.

L. fischeriana d'Orbigny (1845), discussed below, is distinguished by the location of the umbo more towards the posterior, the more rounded outline and the less regular commarginal lamellae.

L. inaequalis d'Orbigny (1845), described below, is distinguished by its short, obliquely truncate posterodorsal margin.

Occurrence. Lower Volgian of southern Germany and the Russian Platform; Middle and Upper Volgian of eastern England.

Subfamily MILTHINAE Chavan, 1969

Genus DISCOLORIPES Wellnhofer, 1964

Type species. Loripes (Discoloripes) gerasimovi Wellnhofer (1964) by original designation. Neuburger Bankkalke, Middle Tithonian, Unterhausen,

West Germany.

Original Diagnosis. (Translation) 'A subgenus of the genus Loripes, with smooth ungrooved margin and circular outline. From Loripes (L.) it is distinguished by the sculpture, which is composed of fine concentric ribs, far apart and somewhat irregularly spaced and by the strongly differentiated structure of the hinge. The dental formula is:

$$\begin{array}{ccccccc} & \text{AI} & & (3a) & & 3b & \\ \text{AII} & & 2 & & 4b & & (\text{PII}) \end{array}$$

Discussion. Discoloripes is here raised to full generic level. In Wellnhofer's diagnosis teeth 2 and 4b have been accidentally misplaced. The only teeth that are well developed are 2, 3b and 4b. 3a may be only weakly developed or absent. The posterior laterals are obsolete, although Wellnhofer has noted a weak PII. Anterior laterals are weak, relatively short and low. AI may be easily seen, but AII may be overlooked under lunule development.

The particularly strongly developed anterior adductor muscle scar would indicate that Discoloripes probably belongs to the family Milthinae. The presence of coarse pustules on the shell interior would partially support this, as Duff (in press) believes that these structures are characteristic of the subfamilies Milthinae and Myrteinae. In his original description Wellnhofer does not note pustules and they are not shown on his illustrated German specimens. However specimens that he includes in the species include Gerasimov 1955, pl. 6, fig. 10, which shows traces of irregular swellings on the shell interior. Specimens described below from the Spilsby basin indicate that the pustules may be

absent or present within species.

Discoloripes fischerianus (d'Orbigny) 1845.

Plate 16, figures 7, 8a, 9a, b, 10, 11, 12, 13, 14a-c, 15, 16a, b, 17, 18, 19, 20, 21a, b. Plate 18 figures 7, 12a-c.

*.1845 Lucina Fischeriana sp. nov. d'Orbigny, p. 458, pl. 38, figs. 31-32.

.1850 Lucina Fischeriana d'Orbigny; d'Orbigny, p. 306

p.1955 Loripes fischerianus (d'Orbigny); Gerasimov, pp. 66-67, pl. 6, 4-9 only.

1964 Mesomiltha fischeriana (d'Orbigny); Wellnhofer, pp. 81-84.

.1969 Loripes fischerianus (d'Orbigny); Gerasimov, pp. 76-77, pl. 6, fig. 6..

Types. Syntypes recorded by d'Orbigny (1845) were collected by Verneuil and Keyserling in 'les rognons isolées des grès chlorites de l'étage oxfordien, à Saragula, environs d'Orenbourg.' They are untraced but may exist in the collections of the Ecole des Mines, Paris.

Diagnosis. Adult shell length 25-30 mm. Subrounded outline with posterodorsal margin truncate. Lunule narrow and deep.

Material. 50 specimens (IGS & SRAK). Common in the S. preplicomphalus Zone and occasional in the S. lamplughii Zone, Upper Volgian, Lower Spilsby Sandstone, Lincs.

Description. Normal adult shell length 25-30 mm. Moderately inflated and thick. Inequilateral. Umbo projecting weakly with small sharp beak. Anterior of shell inflated. Posterodorsal margin weakly to moderately

truncate. Commissural outline subrounded to subcircular. In juvenile specimens, the shell tends to be more elongate, with distinctly inflated anterior region. External ornament of usually clmm slightly raised commarginal lamellae with finer growth lines in between. There is a weakly defined posterior area delineated by increased angulation of the commarginal lamellae. The lunule is very narrow and deep. Escutcheon elongate and lanceolate.

The hinge line is well developed with hinge formula:

	(AII):	(0)	2	4b	n	?
AI	(0)	(0)	3a	0	0	n ?

In the left valve AII is obscured by lunule development, but appears to be bluntly lamellar. There is a weakly developed socket in front of 2 which is cuneiform and vertical and in juveniles is bifid. There is a large triangular socket for 3b. 4b is elongate and lamellar, running along the ventral margin of the nymph. Posterior laterals obscure, and probably only represented by weak swelling at the posterior of the hinge. In the right valve, AI is elongate, blunt and tubercular and situated under the anterior end of the lunule, at the ventral margin of the hinge. There is a feeble socket in front of 3a. 3a itself is subvertical and weak with the dorsal end obscured by the lunule. Large deep triangular socket for 2. 3b stout in adults but juveniles show distinct bifid structure. Socket for 4b poorly defined but separating 3b from the elevated nymph. Posterior laterals obscure if not absent.

The interior of the shell is smooth and without pustules. The adductor scars are deeply inserted in adults, although less distinct in

juveniles. The anterior adductor scar is elongate and recurved and isolated from the pallial line for most of its length. The posterior adductor scar is suboval. The shell margin is thickened below the pallial line and is smooth.

Measurements.

	L	Pp	LE	LLi	LLu	H	B
SRAK, IG.2468	-	-	6	3.5	4	13	3'
2469	15	10	6	-	-	12	3'
2477	32	19	18	11	8	30	7'
2480	13	8	5	-	3	11	5
2481	16	10	7	3	-	13	3'
2482	30	19	15	-	7	25	6'
2494	-	-	8	3	5	15	-
2604	30	14	15	9	9	27	7'
2857	34	23	-	-	-	3	7'
3391	27	20	14	9	7	26	6'
IGS, R26/87	36	26	12	-	-	-	17

Discussion. D. fischerianus has been referred to Loripes by Gerasimov (1955), 1969) and to Mesomiltha by Wellnhofer (1964). Both these genera are regarded by Chavan (in Moore Ed., 1969) as having only a single right valve cardinal tooth. As both 3a and 3b are clearly seen in the Spilsby Sandstone material, the species is here placed in Discoloripes Wellnhofer (1964). The closely related Jagonoma Chavan (1946) has more regular surface ornament of alternating weak and strong commarginal lamellae and 3b is not bifid.

Although the specimens here identified as D. fischerianus appear identical with Russian Platform material in external appearance the internal

features of the latter material are incompletely illustrated. D'Orbigny's original figure of D. fischerianus shows no apparent lunule, but this could be accounted for by the very narrow lunule which is known from the Spilsby specimens. The specimens illustrated by Gerasimov (1955) include internal moulds with deeply impressed adductor scars and pallial line. Specimens show both smooth and pustulose interiors. In the Spilsby material only non-pustulose interiors have so far been encountered. One of the Gerasimov's specimens, pl. 6, fig. 10, is excluded from D. fischerianus and here referred to D. septentrionalis sp. nov., which is a much larger species.

D. cf. inaequalis (d'Orbigny, 1845), discussed below, differs from D. fischerianus by reaching a larger adult size and having a broad, shallow lunule. D. lirata (Phillips 1829, sensu Arkell 1934) is distinguished by the broader lunule, the less pronounced anterior region and the larger adult size.

Occurrence. Upper Volgian of eastern England and the Upper Volgian of the Russian Platform.

Discoloripes cf. inaequalis (d'Orbigny) 1845

Plate 18, figures 8, 9, 10, 11.

cf. 1845 Lucina inaequalis sp. nov. d'Orbigny, p. 459, pl. 309, figs. 4, 5.

p 1936 Lucina sp. nov. aff. (cf. in plate description) inaequalis

d'Orbigny; Spath, p. 123, pl. 46, fig. 1 only.

Types. D'Orbigny stated that the species was collected by Verneuil and Keyserling in the 'grès chlorites de l'étage oxfordien de Saragula, près d'Orenbourg. The present location is unknown but type material may be preserved in the Ecole des Mines, Paris.

Diagnosis. Medium sized lucinid, adult length usually 20 - 40mm, outline sub-quadrate with distinctive obliquely truncate posterodorsal margin. Lunule shallow and broad.

Material. 250 specimens (IGS and SRAK). Common in the Basal Spilsby Nodule Bed in Lincolnshire, the Speeton Clay Coprolite Bed in Yorkshire, Middle Volgian; and in the Lower Spilsby Sandstone, S. primitivus Zone, Upper Volgian, Lincolnshire.

Description. Medium sized lucinid with adult shell length 20-25 mm in the Basal Spilsby Nodule Bed and the Coprolite Bed of the Speeton Clay, and 35-40 mm in the Lower Spilsby Sandstone. Moderately inflated. Commissural outline subquadrate, with relatively low umbo with small prosogyrate beaks situated behind the mid line. Posterior relatively short with obliquely truncate posterodorsal margin. Anterior relatively inflated and deep, with deepest part of the shell well in front of the mid line. Lunule shallow and broadly lanceolate. Escutcheon elongate, with ligament deeply set. External surface ornamented by relatively regular 1-2 mm spaced commarginal lamellae, with finer more irregular growth lines in between. The lamellae are evenly curved but curve more sharply near the posterodorsal margin defining weakly a posterior area.

The hinge line is relatively well developed and from what has been seen corresponds broadly to that of D. fischerianus. The following features have been recognised, AII, AIII, socket for AIV, 3a, 2, 3b, 4b. The posterior lateral region has not been seen clearly. The shell interior is generally smooth and the median groove appears to be absent. The posterior adductor scar is suboval. The anterior adductor scar is very elongate and arcuate. The pallial border may be thickened. However

specimens from the Upper Kimmeridgian of Milne Land, East Greenland (IHGPS) show variation from having smooth to weakly pustulose interiors. The median groove may be absent or present.

Measurement.

	L	H	La	LE	B
SRAK, IG.1844	38	34	26	22	8'

Discussion. Despite the variation in size of adults from the east of England, all the material is comparable to D. inaequalis. The original figures of D'Orbigny (1845) differ from these specimens by showing no lunule and only a weak escutcheon. However both the English and Russian material show the characteristic truncate posterodorsal margin and the well developed shell anterior. Unfortunately the hinges of the Russian specimens are unknown. Early Russian geologists referred late Jurassic lucinids to Lucina lyrata Phillips (1829), eg. Rouiller and Vossinsky, 1848, pl. 1, fig. 31, although the figures show that the specimens were closer to D. inaequalis by having a well developed anterior. The true L. lirata (type from the Hackness Rock of Yorkshire) has a shorter anterior. Specimens from the Upper Kimmeridgian of East Greenland figured by Spath (1936), as L. sp. nov. aff. inaequalis are identical to the larger Spilsby specimens in external view, but unfortunately the hinges are unknown. However I exclude the larger specimen of Spath (pl. 50 fig. 8) which corresponds to D. septentrionalis sp. nov., described below.

Occurrence. Upper Kimmeridgian of East Greenland; Middle and Upper Volgian of eastern England; Middle Volgian of the Russian Platform.

Discoloripes septentrionalis sp. nov.

Plate 17, figures 5a-c, 2, 3, 4a-c, 5

- ?1936 Lucina (?) sp. ind. Spath, p. 124, pl. 48, fig. 7
- p?1936 Lucina sp. nov. aff. inaequalis d'Orbigny; Spath, p. 123,
pl. 50, fig. 8 only
- ?1936 Lucina sp. nov. (?) ind. Spath, p. 124, pl. 50 fig. 9.
- p.1947 Lucina aff. fischeriana d'Orbigny; Spath, p. 43, pl. III,
fig. 7 only.
- p?1955 Loripes fischeriana (d'Orbigny); Gerasimov, pp. 66-67,
pl. 6, fig. 10 only.
- p?1964 Loripes (Discoloripes) gerasimovi Wellrhofer pp. 81-84,
text figs. 52b only.

Types. Holotype, SRAK, JG. 1808, basal shell bed of the Muslingeelv Member of the Hesteelv Fm., H. kochi Zone, Ryazanian. East bank Muslingeelv, 3 km. south of Crinoidbjerg, Jameson Land, East Greenland.

25 Paratypes, SRAK, JG. 1794-1807, 1809-1812, horizon and locality as for holotype. IGS, CE 1929, 2093, 2094, 2100, 2120, 2121, 2190, Subcraspedites band, Runcton Beds, Upper Volgian, Roxham Fm. and CE3776 same horizon, Abbey Station, West Dereham, Norfolk.

Diagnosis. Large lucinid with mature specimens commonly reaching length 65 mm. Outline rounded with slightly produced anterior. Anterior adductor scar very large, very broad and separated for most of its length from the pallial line.

Description. Shell relatively large, with mature adults commonly reaching a length of 65 mm., maximum 90 mm. Shell thick and moderately inflated.

Outline subcircular. Posterior slightly truncated with weakly angular postero-ventral junction. Anterior slightly produced and deeper than posterior. Umbo rounded, low with small sharp prosogyrate beak weakly overhanging the lunular depression in the commissural outline. The lunule itself is short, asymmetrical and deep. In both valves it almost reaches the ventral margin of the hinge, although it is deepest in the left valve. The escutcheon is long and the nymph deeply set, although in some Greenland specimens the ligament can be seen to be projecting slightly beyond the commissural outline. The surface is ornamented with low irregular growth increments, and the posterior area is scarcely differentiated from the flank.

The hinge line is relatively strongly developed, and the formula is as follows:

(AI)	(3a)	0	3b	0	n
(AIII)	(0)	2	0	4b	0 n

The anterior laterals are extremely weak. AI is a short blunt swelling under and to the anterior of the anterior of the lunule. AII is an almost tubercular swelling situated directly under the anterior of the lunule. The floor of the lunule comes almost down to the ventral margin of the hinge line in mature specimens, but may be slightly less deeply set in younger individuals. In the left valve 2 and 4b are prominent. 2 is stoutly cuneiform and subvertical. 4b is narrow but strongly opisthocline with a relatively prominent groove separating it from the long relatively low nymph. In the right valve, 3a may appear weakly, but is obscured by lunular development. 3b is stout and broadly triangular, separated from the nymph by a wide groove. The nymph is deeply set and elongate.

Posterior laterals appear to be completely lacking.

Internally the shell may be smooth or coarsely pustulose. Some pustules are sufficiently large to be called tubercles and may be up to 6 mm broad and 3 mm high (Plate 17, figure 5). There is no trace of an oblique median groove. The adductor scars are moderately deeply impressed. The anterior adductor scar is very long extending almost to the ventral part of the pallial line, although separated from it for most of its length. The scar is very broad and slightly arcuate. The posterior adductor scar is subcircular to suboval with a very slight pallial notch where it joins the pallial line. The ventral margin is smooth, but over much of the anterior part of the shell interior including on the adductor scar, there may be weak slightly arcuate radial striae. The umbonal infilling may give the internal moulds a sharper but more depressed appearance than that of the actual shell.

Discussion. Only one specimen figured in previous literature can be referred to D. septentrionalis with certainty. It was figured by Spath (1947, pl. 3, fig. 7 only) from the beds with Hectoroceras kochi from Jameson Land, East Greenland. He had named it together with another specimen Lucina aff. fischeriana. Material collected on the 1973 Jamesonland Expedition indicate that Spath's material embraced two species, the second of which is as yet undescribed. True 'Lucina' fischeriana is described above under Discoloripes and is readily distinguished by its smaller size and more truncate posterior. Material that Spath had figured earlier (1936) is probably closely comparable, but the hinges have not been studied. Of the two specimens that Spath (1936) labelled L. sp. nov. aff. inaequalis d'Orbigny, that figured on pl. 46, fig. 1 came from the Upper Kimmeridgian of

Milne Land and is very close to L. inaequalis as interpreted here, while the second specimen from the Glauconitic Series above compares in external features with D. septentrionalis. (See discussion of D. aff. inaequalis below.) Further material from the Glauconitic Series of Milne Land has been examined by the author and a specimen is figured on Plate 17 figure 1, which corresponds broadly to the specimen that Spath labelled Lucina sp. nov. ?ind. from the same horizon and locality. Spath (1936) also figured a specimen from a loose block from Aucellaelv, South Jameson Land, which he believed was Portlandian in age, but which may have come from the Lower Cretaceous outcrops to the north. Its large size and outline are characteristic of D. septentrionalis.

In the Moscow region only one large lucinid has been figured by Gerasimov (1955, pl. 6, fig. 10). The specimen came from the D. panderi zone. It was subsequently sketched by Wellnhofer (1964, text fig. 51b) and is a paratype of Loripes (Discoloripes) gerasimovi Wellnhofer, whose holotype came from the Middle Tithonian of Neuberg. The German material is shown by Wellnhofer to have a very elongate anterior adductor scar, but it is much narrower than in D. septentrionalis and is isolated from the pallial line for all of its length. Wellnhofer's sketch of Gerasimov's specimen shows the anterior adductor scar to be the same as in the German material. But Gerasimov's figures are not sufficiently clear to confirm this and the scar could be much broader as in D. septentrionalis.

D. septentrionalis is differentiated from most other lucinids of contemporary age by its distinctive large size and rounded outline.

D. gerasimovi Wellnhofer has a much narrower anterior adductor scar which is isolated from the pallial line. Lucina balmensis Contejean (1860) from the Calcaire à Corbis, Kimmeridgian of Montbeliard, grows as large as

D. septentrionalis but has a distinct broad groove on the exterior running from the umbo to the posterior margin. The dentition is not known.

Occurrence. Upper Volgian of eastern England; Ryazanian and possibly Middle to Upper Volgian of East Greenland. Also possibly from the Middle Volgian of the Russian Platform.

Discoloripes sp. nov?

Plate 18, figures 7, 12 a-c.

Diagnosis. Shell medium size, discoidal with depressed umbo. Lunule narrow and deep. Shell surface smooth except for growth lines. Strong anterior lateral AII. Weak posterior laterals present.

Material. 2 specimens (SRAK). Bed 1 concretions, Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, High Barn Sand Pit, West Keal.

Description. (Based on left valve only) Shell 22-25 mm long, discoidal and moderately inflated. Shell margin is almost circular with depressed umbo and feeble lunular depression in external lateral aspect. Small sharp prosogyrate beak with narrow deep lunule. Escutcheon lanceolate with deeply set ligament. External ornament of growth lines on smooth surface. Posterior area not differentiated.

The hinge line is well developed, the formula is as follows. The right valve dentition is inferred from reflected structures in the left valve.

AII	0	0	2	0	4b	n (PII)	(0)	PIV
	AIII	3a	0	3b	0	n		PIII

AII is short blunt and laminar and situated well below the hinge line to the anterior of the anterior of the lunule. There is a socket to the anterior of 2, while 2 itself is stout, cuneiform and opisthocline. A narrow obliquely triangular socket separates it from the laminar opisthocline 4b which is situated on the margin of the elongate depressed nymph. Posterior teeth are feeble, but PII and PIV are recognised as weak tubercles separated by a minute socket.

The shell interior is pustulose with deeply set musculature. Anterior adductor scar is moderately elongate. Posterior adductor scar suboval. The shell margin is smooth and thickened below the pallial line.

Measurements.

	L	H	LLu	LLi	LE	B
SRAK IG.2605	25	25	5	9	14	6'
2490	22	23	-	-	13	5

Discussion. The two specimens described do not correspond to any late Jurassic or Lower Cretaceous figured material, but they could represent a variety of D. fischerianus. They occur with that species but are distinguished from typical examples by the distinctly circular shell outline and the almost smooth exterior surface.

Superfamily

CRASSATELLACEA Ferussac, 1822.

Family

ASTARTIDAE d'Orbigny, 1844.

Discussion. There has been some discussion as to whether the hinge line in astartids should be regarded as being basically lucinid, that is with

2 cardinal teeth in each valve, 3a, 2, 3b, 4b (eg. Cox and Chavan in Moore Ed. 1969) or corbiculoid (formerly cyrenoid) with 2a, 1, 2b, 3b, 4b (Cossman and Peyrot 1912; Schmidt, 1935; Moret, 1940 and Nicol, 1955). The more conventional idea, put forward by Bernard (1895) and followed here, is that the astartids have a lucinoid hinge although it may be expanded to include 5b. This necessitated 3a and 3b arising from the same lamella.

Boyd and Newell (1969, pp. 908-913) discuss problems in the nomenclature of crassatellacean hinges, especially in the homologies suggested by certain systems of hinge tooth nomenclature. However within a particular superfamily, suggested homologies are probably close to the truth although beyond that superfamily this does not necessarily hold. To be able to discuss heterodont dentitions it is very useful to be able to designate a particular tooth by a symbol, and therefore the Bernard system is used here with the addition of hinge socket information.

Because of the development of certain anterior lateral teeth in some astartidae, it is necessary to increase all the tooth designations in the lucinoid formula by a factor of 2. The reasons are outlined below. One of the specimens figured by Boyd and Newell (1969) is Astarte castanea Say. They indicate teeth in a Steinmann-type formula using the symbol 1 for a tooth and 0 for a socket. This is readily converted into a straightforward Bernard (1895) notation:

AI	III	0	AV	5a	0	5b	0	7b	n		PIII	0	PV
AII	0	AIV		0	4	0	6b	0	n	PII	0	PIV	

It will be noticed immediately that the numbers allocated to the

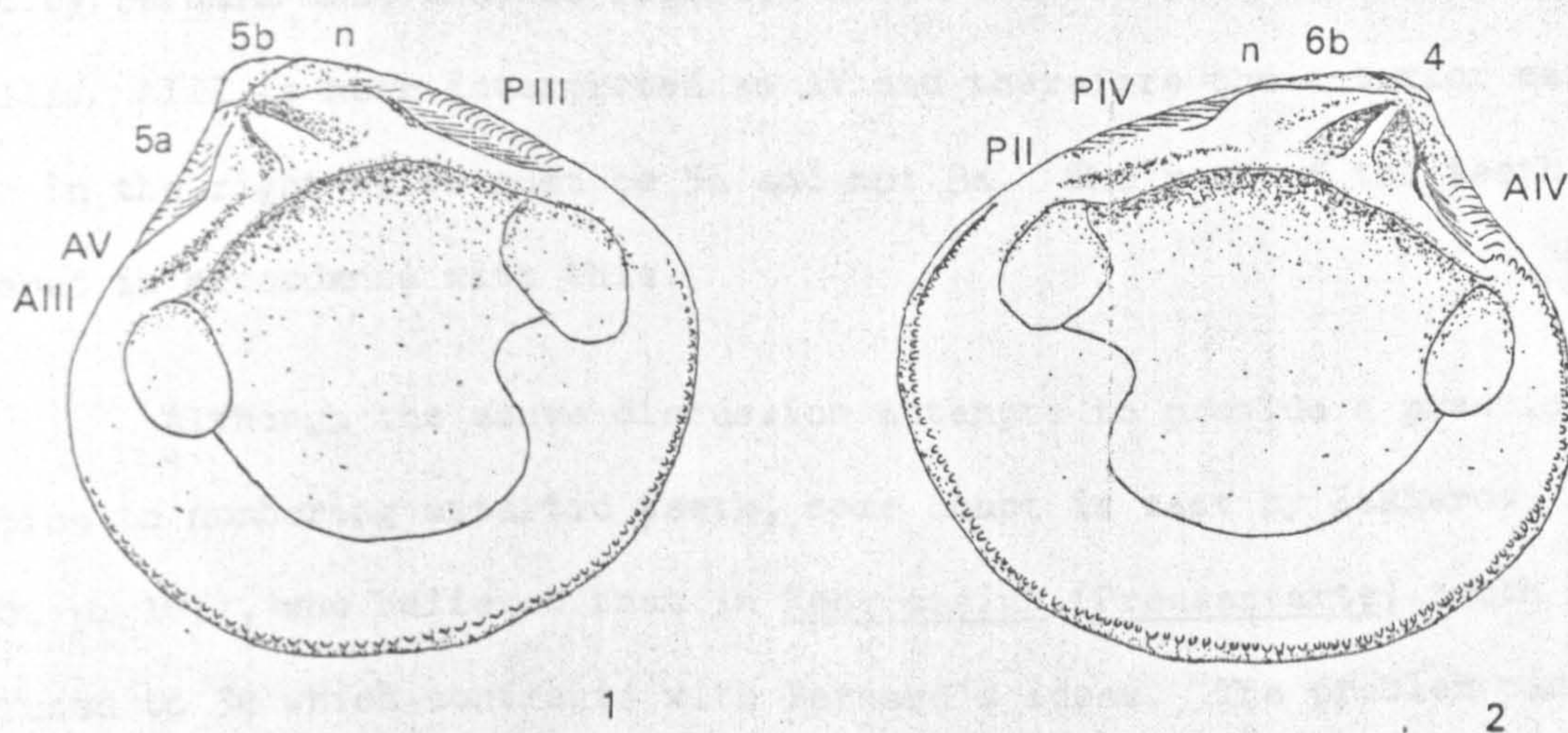


Figure 3.9.

1,2. Neocrassina (Lyapinella) groenlandica sp. nov. 1, paratype, SRAK JG.1192, right valve interior; 2, holotype, JG.1191, left valve interior; Basal conglomerate of Muslingeelv Member, Hesteelv Formation, H. kochi Zone, Ryazanian, 3km. south of Crinoidbjerg, South Jameson Land, East Greenland. xl.

teeth are higher than normal. There are two anterior lateral teeth in each valve and the most ventrally located tooth is in the left valve and must be designated AII. The most dorsal anterior lateral teeth in both valves are commarginal with the floor of the lunule, of which the right valve floor and tooth AV overlaps the left AIV. In the right valve it has been shown by Bernard that what he regarded as 3a erupted from the proximal end of AIII. AIII is here interpreted as AV and therefore the anterior cardinal tooth in the right valve must be 5a and not 3a. The rest of the teeth are numbered in accordance with this.

Although the above discussion attempts to provide a practical solution to numbering astartid teeth, some doubt is cast by Zakharov (1970, p. 103), who believed that in Neocrassina (Pressastarte) tooth AI was fused to 3a which contrasts with Bernard's ideas. The problem can only be resolved by detailed ontogenetic studies which should also provide the answer to the problem of whether astartids have a luncinoid or corbiculoid dentition.

Genus	NEOCRASSINA Fischer, 1886
Subgenus	LYAPINELLA Zakharov, 1970

Type species. Eriphyla (Lyapinella) asiatica Zakharov (1970) by original designation. Upper Jurassic, Middle and Upper Volgian substage of the Northern Urals.

Original diagnosis. (Translation) Shell very rounded, cardinal area wide with well developed 4b and posterior lateral teeth.

Discussion. Lyapinella was introduced by Zakharov (1970) as a subgenus of Eriphyla. Eriphyla ss. has 5a and AV (previously 3a and AIII) fused

and E. (Dozyia) has 5a and AV separated; the shell tends to be subcircular in outline with a low umbo. The type species of Lyapinella, E. (Lyapinella) asiatica has a projecting umbo and relatively suboval outline; 5a and AV are not fused. The hinge of Lyapinella corresponds exactly to that of Neocrassina and the only difference between the two is that Neocrassina is integripalliate, while Lyapinella is sinupalliate. Lyapinella is therefore transferred to a subgenus of Neocrassina. (see Figure 3.9) Its dental formula is:-

AIII	O	AV	5a	O	5b	O	n		PIII
	AIV		O	4	O	6b	n	PII	O PIV

Arkell (1932 p231) has already noted that 'the "Neocrassina" group is continued into the Cretaceous by species with a faint pallial series'; it appears that it was in the late Jurassic however that Neocrassina became sinupalliate thus giving rise to N. (Lyapinella). This is probably in association with a change in life habit from shallow burrowing to deeper burrowing. Amongst the last Neocrassina ss. are included N. ovata (W. Smith) and N. orientalis Zakharov both of Kimmeridgian age. Species that belong within N. (Lyapinella) include Astarte saemanni de Loriol (1868) from the Lower and Middle Volgian of northern Europe; A. duboisiana d'Orbigny (1845) from the northern England Neocomian; A. transversa and A. beaumontii Leymerie 1842) from the Neocomian of northern Europe; and A. obovata from the European Aptian. The stratigraphic distribution of known Lyapinella is shown in figure 3.10.

Neocrassina (Lyapinella) asiatica (Zakharov) 1970

Plate 19 figure 1, 6, 7a,b, 8, 9, 10 a-f.

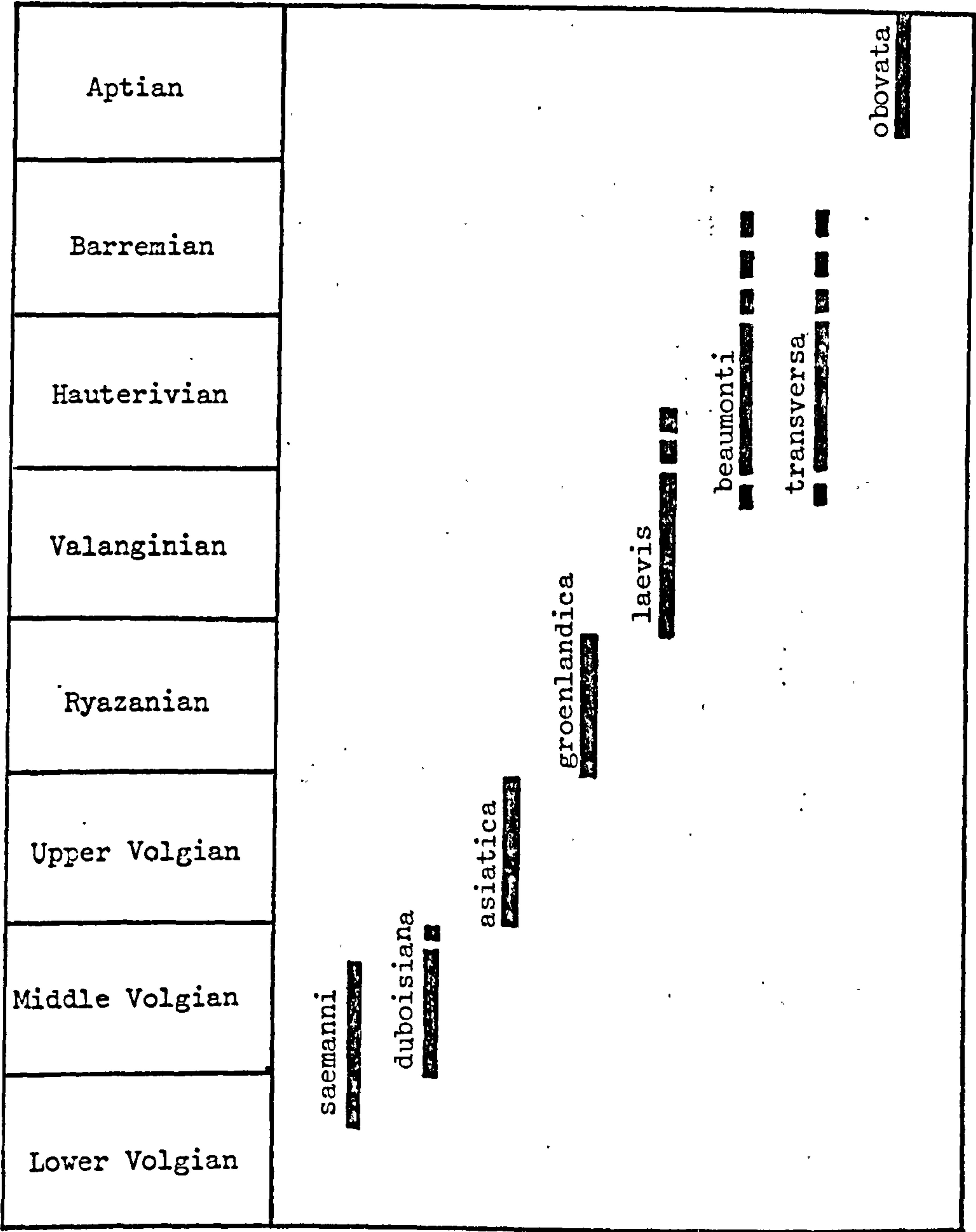


Figure 3.10.

Stratigraphic distribution of *Neocrassina* (*Lyapunella*) in the late Jurassic and Lower Cretaceous of East Greenland, northern Europe and parts of the USSR.

- 1904 Astarte sp. cf. Saemanni de Loriol; Madsen, p. 183, pl. 6, fig. 16.
- p.1936 Astarte aff. saemanni de Loriol; Spath, pp. 115-116, pl. 47,
fig. 2 only.
- .1936 Astarte sp. nov. aff. michaudiana d'Orbigny; Spath,
p. 117, pl. 47, fig. 6.
- ?1964 Astarte Saemanni de Loriol; Sorgenfrei & Buch, p. 131, pl. 7,
figs. 80-82.
- *.1970 Eriphyla (Lyapinella) asiatica Zakharov, pp. 114-115, pl. 14,
fig. 11; pl. 15, figs. 1-6.
- .1974 Eriphyla (Lyapinella) asiatica Zakharov, p. 153, pl. 34, fig. 1

Types. Holotype: Institute of Geology and Geophysics No. 333/479, Zakharov Collection, Strajevskya strajevskyi Subzone, Middle Volgian, River Yatria, north Urals. 146 paratypes: Middle to Upper Volgian of the same area.

Diagnosis. Shell outline suboval, variable, with prominent umbo. Surface ornament of strong commarginal ribs usually becoming gradually weaker after c15 mm from the umbo.

Material. 300 specimens. Common in the Lower Spilsby Sandstone, the Roxham and Runcton Beds, P. oppressus-S. lamplughi Zones, Middle to Upper Volgian of Lincolnshire and Norfolk.

Description. Shell with adult length usually 40-50 mm. Commissural outline usually suboval but variable. Moderately inflated. Umbo prominent and distinctly swept forward. Beak small, prosogyrate and recurved. Lunule short, lanceolate and deep with floor in the left valve overlapping that of the right. Margins evenly rounded except for the slightly indented anterodorsal margin. Escutcheon elongate, lanceolate with prominent long

nymphs. Surface ornament of strong commarginal ribs with fine growth lines superimposed. These usually become gradually weaker after about 15-20 mm. from umbo.

Hinge line strong. Dental formula as given in subgeneric discussion. In the left valve AIV bluntly laminar forming the floor of the lunule. Small socket for 5a rather crowded by lunule growth. 4 large and opsthocline, moderately narrow and triangular with deep obliquely triangular socket behind for 5b. 6b bluntly laminar and almost horizontal backing straight onto the broad nymph plate. PII and PIV bluntly laminar with the latter commarginal with the posterior of the escutcheon, both situated well behind the nymphal plates. There is a deep socket for PIII.

In the right valve AIII and AV bluntly laminar separated by a deep socket for AV. AIII dies out well before 5a which is a triangular projection suspended from the proximal end of AV which is commarginal with the lunule floor. There is a deep triangular socket for 4. 5b is a strong prominent obliquely triangular tooth with a narrow deep and oblique socket for 6b separating it from the nymph. The nymph plate is prominent. There is a single bluntly laminar posterior lateral PIII forming the base of the posterior half of the escutcheon, but dying out before reaching the nymph.

Internally the shell is smooth. The umbonal cavity is large and the subequal adductor scars deeply set on their dorsal sides. The pallial line is weakly impressed and with a small sulcus. The margin may be finely denticulate or smooth.

Measurements.

	L	Lp	LE	LLi	LLu	H	B
SRAK IG.1671	-	38	28	15	-	44	-
1672	45	-	-	-	-	42	13'
1689	33	29	-	-	-	31	-
2344	22	22	14	6	7	-	7'
2856	55	-	-	-	-	46	-
2859	44	40	27	16	14	43	10'
2861	46	36	27	15	14	42	13'
IGS CE3469	42	33	25	12	13	36	10'

Discussion. In Boreal regions 3 neocrassinids occur in the Middle Volgian, all of which are weakly sinupalliate and therefore correspond to Lyapinella (See figure 3.10). They include the type species L. asiatica, recognised by Zakharov and Mesezhnikov (1974) from the North Urals and Siberia, and here recorded also from eastern England and East Greenland. The second species is L. saemanni (de Loriol, 1868) which occurs in the Anglo-Paris basin, central England and East Greenland. It is usually a shorter species with more erect umbo than in L. asiatica, and the ribbing is stronger and extends further over the flank. Some specimens are illustrated on plate 21, figs. 5-7, from the Lower Volgian, Shotover Grit Sands of Swindon, Wilts. The third species L. duboisiana (d'Orbigny 1845), appears at the beginning of the Middle Volgian on the Russian Platform and also occurs in Poland. It is characterised by a much more regularly oval outline than L. asiatica with a low umbo and coarse commarginal ribs which extend over the whole flank. The species is well illustrated by Gerasimov (1955, pl. 5, figs. 1-6), but a specimen is also figured here (Plate 20, figure 13) from the probable

Middle Volgian of Tatarovo.

L. saemanni and L. asiatica appear to be part of a single lineage with L. saemanni occurring in the Lower Volgian and lower part of the Middle Volgian in England, in the Shotover Grit Sands and the Hartwell Clay particularly, and in East Greenland in the Glauconitic Series of Milne Land. L. asiatica appears in the P. oppressus Zone in eastern England and in the Lingula horizon, Laugeites groenlandicus Zone of Milne Land, both of late Middle Volgian age. The species continues into the Upper Volgian S. lamplughii Zone in eastern England, but appears to have been replaced in the Ryazanian by L. groenlandica sp. nov. (see below).

Figured Greenland Lyapinella referable to L. asiatica include that in Madsen (1904) and part of Spath (1936) (see synonymy). The specimens described by Spath from the Glauconitic Series of Milne Lane are referred to L. saemanni, but those from the loose blocks on Aucellaelv, South Jameson Land, including Madsen's figured specimen, are more elongate and appear to be asiatica, and may be derived from strata of late Middle to Upper Volgian age. One specimen that Spath (1936) figured also from a loose block on Aucellaelv was labelled A. sp. nov. aff. michaudiana d'Orbigny and has a strongly prosogyrate umbo, but not as strongly as true A. michaudiana. The Aucellaelv specimen is probably an extreme variant of L. asiatica. Zakharov (1970) was uncertain whether to include Spath's Greenland material under Lyapinella as the published figures did not illustrate the pallial line. However, other specimens examined by the author in the IHGPC collections show that a weak pallial line exists in both L. saemanni and L. asiatica from East Greenland.

Astarte Saemanni de Loriol (Sorgenfrei and Buch 1964)

from the 'Portlandian' of northern Denmark is too smooth for both L. asiatica and L. saemanni, and is closer to L. groenlandica sp. nov. but caution should be observed when identifying single specimens and not assemblages.

L. groenlandica differs from L. asiatica by having a much smoother shell after about 10 mm from the umbo.

Specimens from the basal Spilsby nodule bed are incomplete and therefore are labelled L. aff. asiatica (eg. Plate 19, figure 6.) although it is possible that they may be more closely related to L. saemanni.

Occurrence. Late Middle Volgian to Upper Volgian of eastern England and East Greenland; lower Middle to Upper Volgian of the north Urals and Siberia.

Neocrassina (Lyapinella) groenlandica sp. nov.

Pl. 20 figs. 1-12, pl. 21 figs. 1-4; Text figure 3.9

.1947 Astarte cf. saemanni de Loriol; Spath, pp. 43-44, pl. 4, figs 3-4.

Types. Holotype: SRAK, JG. 1191 and 85 paratypes from the Basal Shell bed of the Muslingeelv Member of the Hesteelv Formation, H. kochi zone, Ryazanian, east bank of Muslingeelv, 3 km south of Crinoidbjerg, Jamesonland East Greenland. Further paratypes in the IHGP collection Copenhagen include that material illustrated by Spath (1947). c1250 paratypes (IGS), from the Mintlyn Beds, H. kochi-S. stenomphalus Zones, Ryazanian, Norfolk.

Diagnosis. Adult shell of medium size, commonly 40-50 mm in length.

Commissural outline suboval with prominent moderately to distinctly prosogyrate umbones. Surface ornament of strong commarginal ribs up to 10 mm from the umbo, thereafter ribbing becomes feeble.

Description. The shell shape and structures are basically as for N. (L.) asiatica but differ in the ornamentation of the exterior which is strong commarginal ribs usually for the first 10 mm, thereafter becoming very feeble, giving a much smoother general appearance to the shell.

Measurements.

	L	Lpp	LE	LLi	LLu	H	B	
SRAK, JG. 1191	59	45	32	18	17	51	16'	
1192	53	43	30	14	16	51	15'	
1193	42	33	23	13	11	36	12'	
1194	43	33	25	14	13	38	11'	
IGS, CE 1554	36	33	-	-	14	34	12'	(fig. 20.4)
1566	37	30	24	11	12	35	-	
2458	42	36	30	16	16	39	-	
2488	27	22	16	7	7	24	7'	
3033	-	-	21	-	-	38	13'	
3041	36	32	25	11	14	37	14'	

Discussion. For comparison of N. (L.) groenlandica with N. (L.) asiatica see discussion above. The apparent size discrepancy between the figured N. (L.) groenlandica from the Mintlyn beds and the Muslingeelv Member is because the larger examples of the former specimens have been damaged during collection and only the smaller ones are sufficiently well preserved for illustration.

N. (L.) laevis (Phillips, 1829), is distinguished from N. (L.) groenlandica by its more erect umbones. It first appears in the topmost Spilsby Sandstone P. albidum Zone at Biscathorpe, but is not fully described here. The type is from the Speeton Clay, but well preserved examples from the upper part of the Claxby Ironstone (Upper Valanginian/Hauterivian) were figured by Woods (1905).

Occurrence. Ryazanian of eastern England and East Greenland.

Subgenus . PRESSASTARTE Zakharov, 1970

Type species. Astarte trembiazensis de Loriol (1901) by original designation. Oxfordian of the Jura Bernois. Almost certainly a junior subjective synonym of Astarte striatocostata (Goldfuss 1826) (= A. phillea d'Orbigny 1850 , A. cepha d'Orbigny 1850 and ?A. trigonarium Dollfuss). The total species range is probably Callovian to Kimmeridgian of northern and central Europe and western Russia.

Diagnosis. (Translation of original) Shell small, subrectangular, planar with sharp beak. Lateral teeth AI and AII distinct, narrow, tooth AI sometimes united with 3a, Lateral teeth PIII and PII distinct narrow and elongate. Cardinal teeth 3b and 2 strongly projecting, tooth 4b more weakly narrow.

Discussion. Pressastarte was introduced by Zakharov (1970) as a subgenus of Neocrassina. The dental formula is the same as for N. (Lyapinella) which is given above. The principal differences are that Pressastarte is generally much smaller and more compressed, the umbonal cavity is very reduced, PIV is less differentiated from the nymph, the lunule is less excavated and the pallial line is integripalliate. In addition there are

features which do not appear to have been recognised in astartids before. These are in the form of horizontal striations on the cardinal teeth which are shown in text figure 3.11, 26, 3. These occur on the anterior and posterior of 4 and 5b, the anterior of 6b and the posterior of 5b. The striations have so far only been recognised on British specimens of Kimmeridgian to Valanginian age. It is not known yet whether these striations have any phylogenetic significance.

Examination of some neocrassinids in the IGS collection indicate that there may be a direct association of N. (Pressastarte) and Neocrassina ss. Some specimens of N. (N.) ovata (W. Smith) from the Kimmeridgian show a distinct break at 15-20 mm from the umbo. Up to this point the shell is usually strongly compressed and smooth with the general features of A. striatocostata, thereafter the features of the adult shell of Neocrassina ss. appear, where the shell becomes more elongate and inflated. Chavan (1952) has already commented on the similarities of the young state of N. (N.) ovata with species that are here referred to Pressastarte, eg. P. nummus and P. pelops. Adults of this type have not yet been seen to bear horizontal striations on the cardinal teeth. At present there are no collections of specimens showing transition from juvenile to adult and the exact relationship between Neocrassina s.s. and N. (Pressastarte) is not yet resolved.

Although Zakharov (1970) lists some Jurassic and Cretaceous species from western Europe that he places in N. (Pressastarte), the name is not yet familiar in the European literature. There appear to be three principal morphological groups of Pressastarte although there are intergradational forms. A brief summary of Upper Jurassic Pressastarte

that have been encountered during this study is included here together with some of their diagnostic features.

Group 1. Forms with a weak to moderately inflated shell with strong ribbing over the whole surface. N. (P.) pelops (d'Orbigny) belongs in this group. A. depressa Roeder (1882) from the Oxfordian of Germany is more inflated at the umbo and has a more erect umbo. A. depressioides Lahusen (1883) from the Oxfordian of Ryazan may be a synonym of A. depressa, and is well illustrated by Gerasimov (1955). N. (P.) woldsi sp. nov. from the Upper Volgian becomes more finely ribbed than pelops after about 7-10 mm from the umbo, and has a more inflated ventral margin. N. (P.) senecta Woods from the Valanginian Claxby Ironstone of Lincolnshire, grows to a greater adult size, length c20 - 24 mm, than N. (P.) pelops.

Group 2. Weakly inflated shell, flattened, with strong ribbing over the whole exterior surface. This group is characterised by Astarte nummus Sauvage (1871), the type of which was clearly refigured by Arkell (1932) from the 'Calcaire Marneaux du Mont des Boucards, Boulonnais'. Arkell recognised the species from the Corallian of the Dorset Coast and de Loriol (1875) from the Lower Kimmeridgian of Boulogne. It is also common (IGS, SMC, BMNH) in the Swindon and Hartwell Clays (Middle Volgian) of Central England. Astarte minima Rouillier (1846) (non Phillips) from the ?Upper Kimmeridgian of the Moscow region may be a synonym of nummus.) N. (P.) pressula Zakharov (1970) from the Volgian of North Siberia is more coarsely ribbed than N. (P.) nummus.

Group 3. Weakly inflated shell, flattened, with strong ribbing only on umbonal region, dying out to a smooth flank. N. (P.)

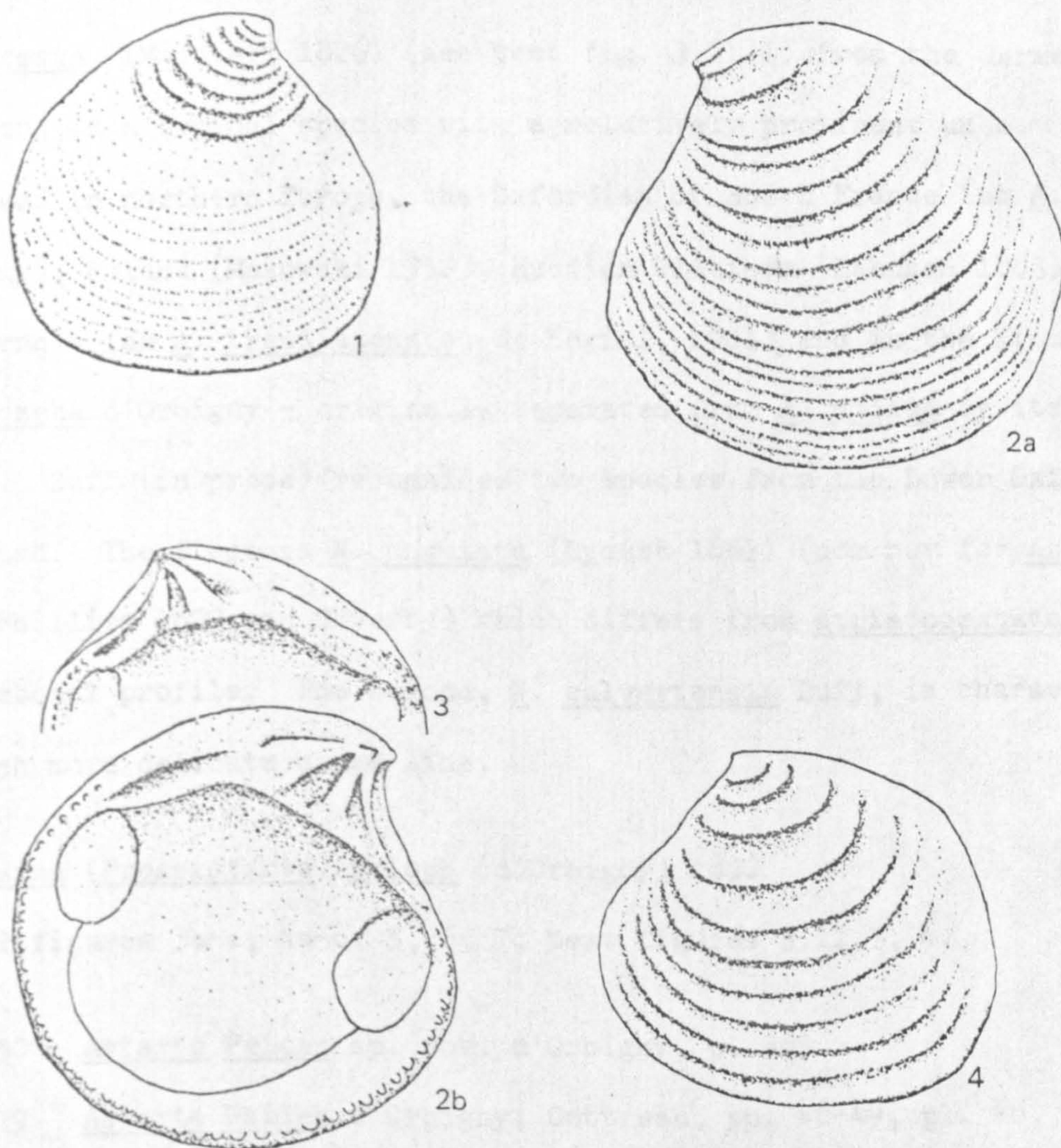


Figure 3.11

- 1, Neocrassina (Pressastarte) striatocostata (Goldfuss). SMC J.28108. Kimmeridge Clay, unhorizoned, Market Rasen, Lincs.
- 2a, b. Neocrassina (P.) woldsi sp. nov, Holotype. SRAK IG.2348, left valve interior and exterior, Lower Spilsby Sandstone,, S. preplicomphalus Zone, Upper Volgian, West Keal, Lincs.
- 3, 4. Neocrassina (P.) pelops (d'Orbigny). 3, SRAK IG.1561, internal view of right valve; 4, IG.2177, external view of left valve; Basal Spilsby Nodule Bed, Middle Volgian. Nettleton, Lincs. All x3.

striatocosta (Munster, 1826) (see text fig. 3.11.1) from the German Oxfordian, is a typical species with a relatively prominent umbo. It is widespread in northern Europe, the Oxfordian of north France (as A. philea d'Orbigny), Poland (Makowski 1952), Russian Platform (Lahusen 1883) and the Jura Bernois (as A. trembiazensis) de Loriol, 1901) and in the Kimmeridgian (as A. cepha d'Orbigny - originally separated from A. philea by its smooth margin). Duff (in press) recognises two species from the Lower Oxford Clay of England. The first is N. ungulata (Lycett 1863) (nom. nov. for Astarte lurida Phillips 1829 non Sowerby) which differs from striatocostata by its lower umbonal profile. The second, N. calvertensis Duff, is characterised by a much more delicate hinge line.

Neocrassina (Pressastarte) pelops (d'Orbigny) 1850

Plate 22 figures 3a-c, 4a-c, 5, 6, 7, text figures 3.11 3, 4.

.1850 Astarte Pelops sp. nov. d'Orbigny, p. 363.

p.1929 Astarte Philea d'Orbigny; Cottreau, pp. 48-49, pl. 46, figs 1, 2.

Types. Cottreau (1929) figures one of d'Orbigny's syntypes (No. 3662) from the Corallian of Neuvizy. In the discussion he places it in synonymy with A. philea with which it was found.

Diagnosis. Shell small, weakly to moderately inflated, not flattened, except slightly on the umbo. Commissural outline subquadrate to subovoidal.

Strong commarginal ribs evenly spaced over whole shell surface though slightly more widely on the first 5 mm.

Material. 60 specimens, SRAK, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.

Description. Shell small and thick with normal adult length c15 mm.

Weakly to moderately inflated, not flattened except for first 5 mm.

Commissural outline subquadrate to subovoidal, with prominent umbo situated well forward with small almost recurved sharp beak. Behind the beak the shell margin rounds evenly to the slight angulation of the posteroventral margin. Ventral margin is slightly flattened. Lunule is short lanceolate and shallow with floor rounded against the wall without angulation. Escutcheon elongate, lanceolate with short weakly developed nymphs visible. External shell surface ornamented by coarse angular commarginal ribs spaced about 1 mm apart over most of the shell but slightly coarser on the first 5 mm. The ribs are covered with fine growth lines.

The hinge line is quite strong. In the left valve AIV is short and laminar, commarginal with the lunule floor. There is a small triangular socket for 5a. 4 is prominent and narrowly triangular, extending to the ventral border of the hinge. It bears horizontal striations on both the anterior and posterior surfaces. Large obliquely triangular socket for 5b. Oblique laminate 6b striated on its anterior surface, and situated on the anterior margin of the moderately developed nymph plate. PII and IV are laminar, dying out at the distal end of the nymph plate. PIV is commarginal with posterior of escutcheon floor. Large elongate socket for PIII.

In the right valve, AIII is laminar, extending to the foot of 5a. There is a large socket for AIV. The laminar AV, commarginal with the lunule floor reaches to the beak. 5a is small, subvertical not reaching the ventral margin of the hinge and striated on its anterior surface. There is a large triangular socket for 4. The stout obliquely triangular 5b is striated on both the anterior and posterior surfaces and reaches the

ventral margin of the hinge. There is a shallow narrow oblique socket for 6b. The nymph plate is narrow. PII is elongate, laminar, commarginal with the floor of the escutcheon and merges into the posterior of the nymph.

The interior of the shell is smooth. Umbonal infilling shallow. The dorsal edges of the adductor scars are deeply set. The anterior adductor scar is suboval, while that of the posterior is closer to subcircular. The pallial line integripalliate. The margin may be smooth or crenulate.

Measurements.

	L	Lp	LE	LLi	LLu	H	B
IG.1561	15	12	9	4	5	13	5
2177	14	12	10	4	5	13	4

Discussion. N. (P.) woldsi sp. nov. (described below) is distinguished from N. (P.) pelops by having finer commarginal ribbing after 7 - 10 mm from the umbo and has a more inflated ventral margin. N. (P.) senecta (Woods) from the Claxby Ironstone grows to a greater adult size (L. 20-24 mm) than N. (P.) pelops.

Occurrence. Oxfordian of southern England and north France. Middle Volgian of eastern England.

Neocrassina (Pressastarte) woldsi sp. nov.

Plate 22, figures 1a-c, 2a-c, text figures 3.11. 2a, 2b.

Diagnosis. Shell small, commissural outline suborbicular to suboval. Moderately inflated, not flattened, except at umbo. Strong commarginal

ornament widely spaced on flat umbo, becoming much finer on the lower part of the flank.

Types. Holotype: SRAK IG.2348, and 3 paratypes, bed 1 concretions, Lower Spilsby Sandstone, S. preplicomphalus zone, Upper Volgian, High Barn, West Keal, Lincs. 2 paratypes:(SRAK) from the same horizon, 1 km north of Spilsby and 800 m west of Harrington Hall. 36 paratypes (SRAK and IGS) in erratic blocks of Lower Spilsby Sandstone associated with Paracraspedites, and Subcraspedites, Leziate Sand Pit, Norfolk. 2 paratypes (SRAK) in bed 6 concretions, Lower Spilsby Sandstone, S. lamplughii zone, Nettleton, Lincs. 6 paratypes (SRAK) in preservation of bed 4 concretions S. primitivus zone, Upper Volgian of the same locality.

Description. The general size and shape corresponds closely to the description given above for N. (P.) pelops. The principal differences are the crowding of the mid and distal flank ribbing, and the more inflated ventral margin.

Measurements.

	L	Lp	LE	LLi	LLu	H	B
IG.2353	14	12	9	4	5	13	4
2348	17	13	11	5	6	16	5

Discussion. The comparison of N. (P.) woldsi with other species is shown in the discussion of N. (P.) pelops.

Occurrence. Middle to Upper Volgian of eastern England.

Genus

NICANIELLA Chavan, 1945

Type species. Astarte communis Zittel and Goubert (1861) by original designation. L. Kimmeridgian, northern France.

Discussion. Chavan (1945 and in Moore Ed. 1969) states that there is no 3a present in Nicaniella sensu lato, which embraces also the subgenus Trautscholdia Cox & Arkell (1948). However in describing the type species, Chavan (1952, p. 59) indicates that there is a 'trace of 3a embedded in the lunule' (litteral translation). Duff (in press) regards the presence of 3a indicative of Trautscholdia s.s. However specimens regarded here as Trautscholdia, are those which have distinctly constricted and inflated umbones, and which have the site of 3a almost completely obscured by lunule development.

In an attempt to clarify the situation, the following points are made. The dental formula for Nicaniella s.l. is as follows:

AIII	0	AV	(5a)	0	5b	0	(7b)	n		PIII
	AIV		(0)	4	0	6b	(0)	n	PII	PIV

The anterior and posterior lateral teeth are well developed. However of the cardinal teeth, only 4, 5b and 6b are strong and have deep sockets. 5a may be present weakly or absent. 7b is small but usually present. In Nicaniella s.s. 5a may be absent or present. In Trautscholdia it is almost absent because growth of the lunule has obscured the site of development. The most obvious feature for distinguishing the difference between Nicaniella and Trautscholdia was recognised by Chavan (in Moore ed. 1969). Nicaniella has a convex to straight posterodorsal margin,

while in Trautscholdia it is distinctly concave, and the umbo is distinctly constricted and inflated.

Although the above definitions make it easy to allocate individual specimens to one subgenus or the other, the naming of species assemblages from particular horizons is not clear cut. It is possible to find a single species assemblage spanning the subgeneric boundaries. Such assemblages have been illustrated by Roeder (1882) and Duff (in press). Roeder figured Astarte multiformis Roeder from the German Oxfordian. The bulk of the specimens shown belong to Nicaniella s.s., while some labelled var. inaequistriata have the distinct concave posterodorsal margin of Trautscholdia. Duff figures specimens labelled Trautscholdia phillis (Cottreau). The bulk of the specimens in his scatter diagram belong to Nicaniella s.s., while only a few are Trautscholdia. Material described below from the Spilsby Sandstone is more clear cut than the examples just mentioned and falls into one subgenus or the other without overlap.

Subgenus

NICANIELLA Chavan, 1945

Diagnosis. (Emended) Shell small, trigonal to subquadrate in outline with moderately prominent umbones. Posterodorsal margin convex or straight. Dental formula as given above with 5a weakly developed or absent.

Nicaniella (Nicaniella) mnewnikensis (Milaschewitsch) 1881

Plate 22, figures 11b-d, 12a-c, 13, 14, 15a-c, 16, 17, 18, 19.

.1861a Astarte Voltzii Goldfuss; Trautschold, pp. 81-82, pl. 7, figs.

5a-d

1861a Astarte minima Phillips; Trautschold, p. 82, pl. 7, fig. 6.

p.1881 Gouldia mnewnikensis sp. nov. Milaschewitsch, p. 114.

.1955 Astarte mnevnikensis Milaschewitsch; Gerasimov, pp. 63-64,
pl. 4, figs 1-4.

.1969 Astarte mnevnikensis Milaschewitsch; Gerasimov, p. 75, pl. 6,
figs 7, 8.

Types. Milaschewitsch (1881) listed the figures of Astarte bouchiana d'Orbigny, A. minima Phillips (sensu Trautschold) and A. veltzii Goldfuss (sensu Trautschold) as syntypes. I exclude the specimen of d'Orbigny from the synonymy. When it is firmly established that Trautscholds' material has been lost, then a neotype can be selected from the specimens figured by Gerasimov (1955)

Diagnosis. Shell small, subtrigonal with distinctly inflated umbo. Adult ornament of 10 - 13 coarse commarginal ribs, evenly rounded and only weakly truncate at the posterior in early growth stages. Hinge with diminutive 5a present.

Material. 37 specimens (SRAK) Basal Spilsby Nodule Bed, Nettleton, Lincs.

Description. Shell small with maximum adult shell length just in excess of 14 mm. Specimens usually 10 - 12 mm in length. The juvenile shell is strongly inflated but the degree of inflation decreases with age. The outline is subtrigonal and relatively orthogyrate in adults though tending to be more distinctly prosogyrate in young specimens. Beaks small and prosogyrate. Anterodorsal margin straight. The lunule is cordate and shallowly impressed. The escutcheon is elongate and broadly lanceolate. The outline is trigonal with a bluntly rounded posterior and slightly more rounded anterior. The surface ornament is composed of 10 - 14 coarse commarginal ribs, trigonal to slightly rounded in cross section.

The hinge line is strong immediately under the beaks, but weaker in the region of the lateral teeth. In the left valve AIV is laminar, commarginal with the lunule floor. There is a weak groove for 5a. 4 is strong and triangular reaching the ventral margin of the hinge line. There is a deep triangular socket for 5b. 6b is strong but obliquely triangular to laminar, also reaching the ventral margin of the hinge. 6b backs onto the nymph which is approximately the same length and slightly depressed, PII and IV are very elongate and laminar, separated by the socket for PIII. PIV is confluent with the escutcheon and almost runs into the nymph, but is slightly raised above it.

In the right valve AIII and AV together with the socket for AIV are laminar and slightly concave, paralleling the lunule floor with which AV is commarginal. 5a is usually represented by a fine laminar ridge on the proximal end of the lunule margin. Also under the lunule a weak buttress may be seen which may represent the basal part of the tooth. There are large deep triangular sockets for 4 and 6b symmetrically placed in front and behind the prominent erect triangular 5b. The nymph and 7b are barely separated from the single posterior lateral PIII which is commarginal with the escutcheon margin.

Internally the shell is smooth. There is a short bulbous umbonal cavity. The subequal adductor scars are deeply impressed in their dorsal margins and slightly elevated at the ventral edges. Integripalliate. Margin may be smooth or denticulate.

Measurements.

	L	Lp	H	B
SRAK IG. 3440	12	8	10	4'
3444	-	-	11	5
2186	12	-	12	-
2178	10	7	9	8

Discussion. Milaschwitsch erected Gouldia mnewnikensis based on the figures of Astarte bouchiana d'Orbigny (1845), Astarte vultzii Trautschold (1861a) non Golduss and A. minima Trautschold (1861a) non Phillips. Trautscholds figures differ distinctly from d'Orbigny's. A. bouchiana has a strongly truncate posterior, while the figures of A. vultzii and minima have a more circular outline and strong ribbing. Trautschold's specimens came from the 'dark sands of Mniowniki'. Gerasimov has confidently taken Milaschewitsch's species to be of Middle Volgian age and has also excluded d'Orbigny's figure from the synonymy list. The specimens that he figures (1955, pl. 4, 1-4) have a strongly inflated shell and coarse ribbing. They are generally much smaller than fully grown Spilsby Sandstone examples, although small Spilsby Sandstone specimens appear identical.

N. (N.) extensa (Phillips 1829) (= A. mysis d'Orbigny 1850) from the Oxfordian of the Yorkshire coast has a more truncate posterior than N. mnewnikensis and has slightly finer ribbing.

N. (?N.) sauvagei (de Loriol, 1875) from the Sequanien of Boulogne is very small and extremely inflates. It may be a form transitional to Trautscholdia.

Occurrence. Middle Volgian of eastern England and the Russian Platform.

Subgenus

TRAUTSCHOLDIA Cox & Arkell, 1948

Diagnosis. (Emended) Shell small, trigonal in outline with very prominent swollen umbones. Posterodorsal margin concave. Dental formula as given for genus, but with 5a normally obscured by lunule development.

Nicaniella (Trautscholdia) claxbiensis (Woods) 1906

Plate 22, figures 8a-d, 9a-d, 10a-d, 11a only.

* v.1906 Astarte claxbiensis sp. nov. Woods, pp. 108-109, pl. 14, figs 25-28.

Types. Woods (1906) mentions at least 5 syntypes preserved in the Sedgwick Museum, Cambridge, and the Yorkshire Museum, which come from the Claxby Ironstone of Benniworth Haven and the Spilsby Sandstone of Donnington. A specimen from the Claxby Ironstone, Valanginian, (SMC B.11355) which was figured by Woods 1906, pl. 14, fig. 26 is designated here as lectotype. Woods' figure is twice natural size.

Material. 10 specimens. 3 specimens, Basal Spilsby nodule bed, Middle Volgian, Nettleton, Lincs. 2 specimens associated with Paracraspedites in erratic blocks of Lower Spilsby Sandstone, P. oppressus Zone, Middle Volgian, Leziate Sand Pit, Norfolk. 5 specimens from bed 1 concretions, Lower Spilsby Sandstone, High Barn Sand Pit, West Keal.

Diagnosis. Small size with prominent swollen umbones. Anterior and posterior dorsal margins concave. Relatively fine but strong commarginal ribs. 5a normally obscured by lunule development.

Description. Shell small with maximum adult length 14 mm and height 14 mm. Commissural outline suboval with slightly deeper posterior than anterior.

The umbones are very strongly inflated and constricted, although the degree of inflation of the shell decreases with age. The beaks are small, prosogyrate and weakly overhanging. Posterodorsal and anterodorsal margins are concave. Anterior margin rounded, ventral margin weakly inflated, posterior margin slightly truncate. Gently depressed cordate lunule. Escutcheon lanceolate. Exterior surface ornamented by relatively fine, regular commarginal ribs up to an estimated 25 in number. Hinge and interior as in N. (N.) mnevnikensis differing only by having 5a almost completely obscured by lunule development.

Measurements.

	L	Lp	H	B
SRAK IG. 2347	12	8	11	5'
2346	14	8	15	6'
3439	11	9	10	-
SMC B. 11354 *	9+	6	8+	4'

* taken from photographs.

Discussion. N. (T.) claxbiensis differs from N. (T.) cordata (Trautschold 1860, =Astarte cordiformis Rouillier 1846, non Deshayes) from the Oxfordian of the Moscow region, by having a less constricted umbonal region and more numerous finer ribs on the flank. N. (T.) claxbiensis also occurs in the Swindon Clay, the Hartwell Clay (IGS) and in the basal Claxby Ironstone, but no specimens have yet been seen from these horizons, or from the Basal Spilsby Nodule Bed, which compare in size with the particularly large specimen illustrated here (Plate 22, figure 9) from the Lower Spilsby Sandstone.

Distribution. Middle Volgian to Lower Valanginian of central and eastern England.

Superfamily	ARCTICACEA Newton, 1891
Family	ARCTICIDAE Newton, 1891
Genus	ANISOCARDIA Munier-Chalmas, 1863
Subgenus	ANTIQUICYPRINA Casey, 1952

Discussion. The occurrence of the subgenus in the Middle Volgian to Ryazanian of the Spilsby basin extends its range to the Lower Cretaceous: it was previously known from the Middle Jurassic.

Anisocardia (Antiquicyprina) lincolnshirensis sp. nov.

Plate 22, figures 20, 21a-c, 22a-c, 23a-c, 24, 25, 28a,b.

Types. Holotype SRAK IG.2144 and 170 paratypes from the basal Spilsby nodule bed, Middle Volgian, Nettleton, Lincs. Paratypes also from the Mintlyn Beds, H. kochi Zone, Ryazanian of West Dereham, Norfolk.

Diagnosis. Shell of small to medium size, maximum adult length usually 25 mm. Commissural outline subcircular to suboval with projecting umbo. 3b obliquely triangular and stout.

Description. Shell of small to medium size, moderately thick and distinctly inflated. Adults usually 20-25 mm in length. The commissural outline is subcircular to suboval. The umbo is prominent with small incurved prosogyrate beak. The lunule is not depressed but is circumscribed by a delicate groove. The escutcheon is obsolete. The flank is ornamented with fine regular growth lines which pass across the lunule. There is no distinct posterior area. Hinge line well developed and moderately broad.

Dental formula as follows:

AI	0	AIII	3a	0	1	0	3b	0	(?5b)	n	PI	0	PIII
	AII		AIV (0)	2a	0	2b	0	4b	(0)	n		PII	

In the right valve AI is short and bluntly laminar with 1 short and acutely laminar fused on the proximal end and located immediately to the anterior of the beak. There is a deep elongate socket for 2a and AIII is laminar and separate from the margin and bears a weak acutely laminar 3a on the proximal end. 3b is stout, obliquely triangular, bifid and located directly under the umbo. The nymph plate is prominent, broad and smooth but with weak traces of 5b as a short laminar tooth. PI is elongate and bluntly laminar and situated well to the posterior of the nymph. There is a deep socket for PII and PIII is laminar, acute and commarginal with the posterodorsal margin. In the left valve AII is short with 2a as a short laminar projection at the proximal end. It is weakly connected to the anterior part of the chevron shaped 2b which is located directly under the beak. There is a deep socket for AIII and AIV is acutely laminar forming the anterodorsal margin. There is a deep obliquely triangular socket for 3b. 4b is narrowly cuneiform and separated from the narrow nymph plate by a weak groove. The laminar PII is commarginal with the posterodorsal margin.

The shell margin is smooth, the adductors are weakly impressed and suboval. There may be a weak pallial indentation.

Measurements.

		L	Lp	H	B
SRAK IG.	3216	19	13	19	7'
	3249	27	19	22+	10'
IGS CE	2505	25	16	24	9'

Discussion. Late Jurassic and early Cretaceous anisocardiids are not well known. In general outline A. lincolnshirensis has a more prominent umbonal region than the 'Portlandien' forms of the Yonne, like A. cottaldini and A. letteroni (de Loriol and Cotteau (1868), but has the same commarginal ornament as these forms which contrasts with the radial ornament of A. (Anisocardia) elegans (Munier-Chalmas) from the Kimmeridgian. This latter species has tooth 1 situated to the anterior of 3a as shown by Cox (1947, p. 145). But in the Spilsby specimens there is considerable overlap of these teeth and 1 is nearly underneath 3a. Casey (1952, p. 152) notes that in the genus Anisocardia 3a may descend towards and almost touch 1, but these two teeth are subparallel and isolated in A. lincolnshirensis. Anisocardia buckmani Cox (1925) from the basal Shell Bed of the Portland Stone in Dorset is smaller and has a more truncate posterior. A. sandringhamensis sp. nov. (described below) from the Mintlyn Beds of Norfolk has more depressed umbones and 3b is narrowly cuneiform and almost horizontal.

Occurrence. Middle Volgian to Ryazanian of eastern England.

Anisocardia (Antiquicyprina) sandringhamensis sp. nov.

Plate 22, figures 26 a-c, 27.

Types. Holotype, IGS WA 3283, from the Mintlyn Beds, H. kochi Zone, Ryazanian, Flood Relief Channel, West Dereham, Norfolk. Paratypes from the same horizon (IGS) and from erratic blocks of Middle and (?) Upper Volgian age (IGS, SRAK), Leziate, Norfolk.

Diagnosis. Commissural outline suboval with low umbo. 3b narrowly cuneiform and subhorizontal.

Description. As for A. (A.) lincolnshirensis, but differs in the following

features: the commissural outline is normally suboval with a low umbo and small prosogyrate beaks, the hinge line is more delicate and the tooth 3b is narrowly cuneiform and almost horizontal.

Measurements.

	L	H
IGS WA 3283 Holotype	23	21+

Discussion. See description above and discussion of A. (A.) lincolnshirensis.

Occurrence. Middle Volgian to Ryazanian of eastern England.

Genus

HARTWELLIA Kitchin, 1926

Discussion. Kitchin (1926) believed that Hartwellia represented a blind alley of astartid evolution in the late Jurassic. Casey (1952) showed that the origin of the genus was probably with the Middle Jurassic Staffinella of the Scottish Great Estuarine Series, and which gave rise to a flourishing line of Upper Cretaceous veneridae. This latter view is upheld here. It is furthermore suggested that Hartwellia may embrace at least two separate lineages passing across the Jurassic-Cretaceous boundary. Hartwellia (H.) hartwellensis appears in the Lower Volgian sandy facies of central England and continues through the Middle Volgian into the Upper Volgian. The species has been well illustrated (Kitchin 1926; Cox 1944; Casey 1952). A possible direct link between H. (H.) hartwellensis and H. (Tealbya) is described here. It appears in the Mintlyn Beds (Ryazanian) and is named H. (H.) mintlyni but shows transitional features between the two subgenera, especially in the position of tooth 1 which has moved closer in between 3a and 3b than in Hartwellia s.s. H. (H.) eventually gives rise to the

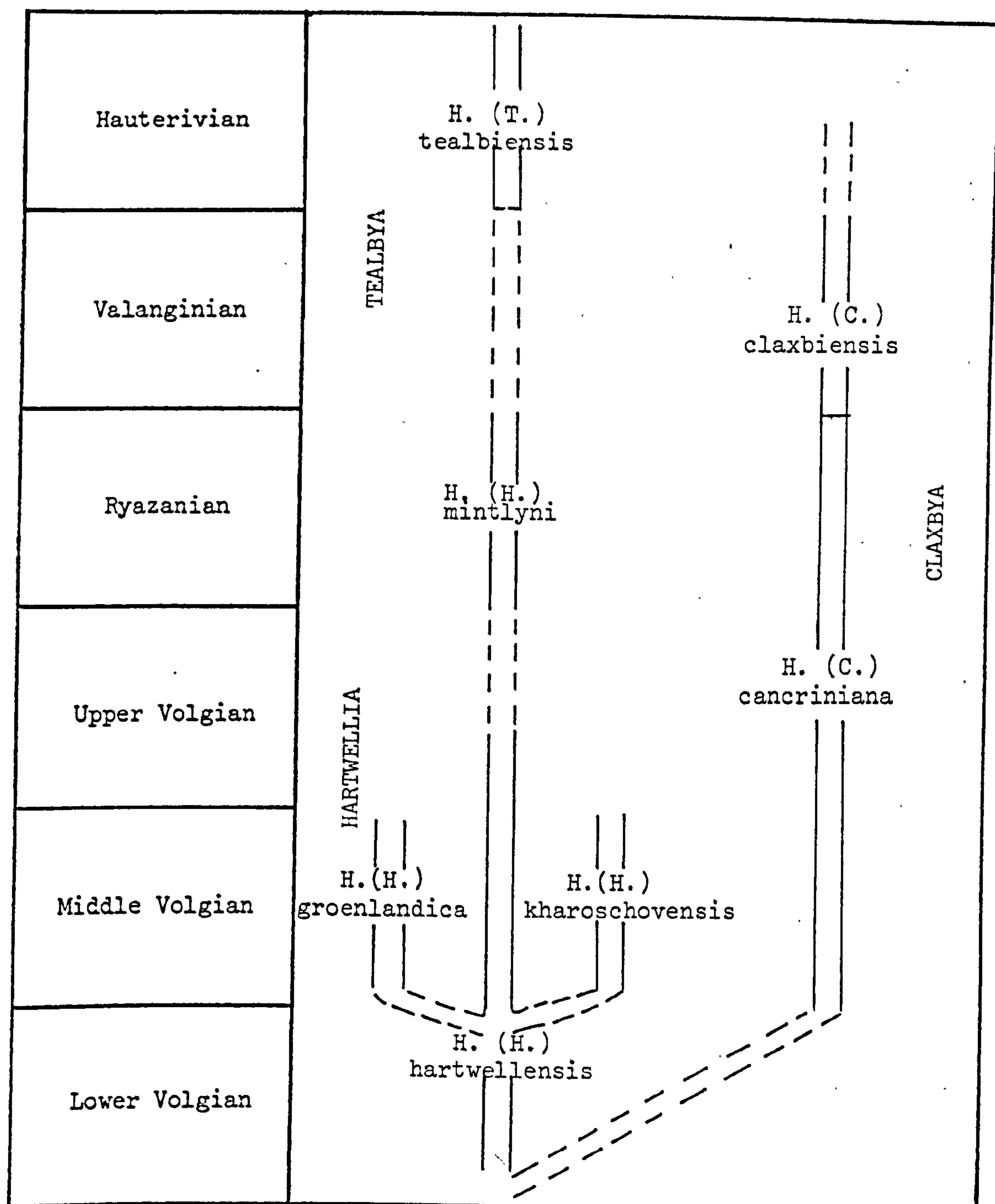


Figure 3.12

Suggested phylogenies for late Jurassic and early Cretaceous hartwellioid bivalves.

Hauterivian species H. (T.) tealbiensis Casey and H. (T.) pseudangulata Casey in the British Isles (See Figure 3.12).

In the Sandy Shales (horizon of Spath, 1936) in Milne Land, East Greenland, occurs a hartwelliid originally named Pseudotrapezium groenlandicum Spath, but which is Hartwellia s.s. Its association with Crendonites may suggest a late Middle Volgian age. A further Middle Volgian species is H. (H.) kharoschovensis (Rouillier and Vossinsky) from the Russian Platform. It is believed that these two species may represent minor branches off the principal Hartwellia-Tealbya lineage. A second lineage which crosses the Jurassic Cretaceous boundary is Claxbya subgen. nov. which is described below (See Figure 3.12).

Hartwellia (Hartwellia) mintlyni sp. nov.

Plate 23, figures 3-6.

Types. Holotype IGS WA 3423 and WA 3412 (external and internal moulds of the same specimen), Mintlyn Beds, H. kochi Zone, Ryazanian, Flood Relief Channel, West Dereham, Norfolk. 13 paratypes (IGS) from the same horizon and 2 further paratypes from the S. stenomphalus Zone of the King's Lynn Bypass.

Diagnosis. Adult shell 40 - 50 mm in length and moderately inflated.

Up to 25 mm length, shell weakly inflated with up to 10 mm length having commarginal ribbing, thereafter becoming smooth. Posterior margin gently rounded and posterior carina feebly developed.

Description. Adult shell of medium size, normally 40 - 50 mm in length.

Elongate, with commissural outline suboval with slightly projecting umbo and small beak located about 1/3 the length of the shell from the anterior.

The shell is moderately inflated and thick in the adults, but juveniles are thin and weakly inflated. Lunule is weakly indented and not sharply delineated. The escutcheon is sharply marked by a change in slope of about 90° . The posterior margin is not truncate but gently rounded and the posterior carina is only weakly seen. The whole flank in the adult is ornamented with close set, fine growth lines, giving an almost smooth shell. However the early shell ornament indicates that individuals up to about 10 mm in length are ornamented by coarse commarginal ribs.

The hinge line is well developed. The formula is:

AI	0	AIII		3a	0	1	0	3b		PI	0	PIII
(0) AII		0	AIV	0	2a	0	2b	0	4b		PII	

In the right valve the anterior laterals are short. AI is low, blunt and laminar, with deep elongate socket for AII on the dorsal side. PIII is a narrow laminar tooth separated from the anterodorsal margin by a thin groove. Its proximal end merges with the short narrow laminar 3a. Tooth 1 is large and triangular occupying most of the space between 3a and 3b. It is weakly differentiated from the proximal end of AI. 3b is a narrow, opisthocline, weakly bifid and, cuneiform. There is a wide socket for 4b. The nyrph is wide and elevated with lateral callosity. The ligament groove extends about half the length of the escutcheon. PI is elongate stout and bluntly laminar, with a deep socket separating it from PIII which is confluent with the escutchen margin. Both posterior laterals extend almost to the posterior margin of the shell.

In the left valve AII is short and laminar, with its proximal and elevated to form 2a. AIV is confluent with the shell margin and extends

to the beak. There is a prominent groove for AIII and also weak traces on the ventral side of tooth AII of a socket for AI. Directly below the beak is situated the chevron shaped 2b. 2b2 is more elongate and stout, but 2b1 is shorter and passes into 2a with only weak constriction. 4b is a narrow laminar tooth on the side of the nymph. PII is elongate and stout.

Internally the shell is smooth. The relative size of the umbonal infilling and the degree of prosogyricity increase with the size of the shell. The adductor scars are moderately impressed and subcircular to suboval. The pallial line is distinct and shows a small pallial sinus. The shell margins are smooth.

Measurements

	L	Lp	H	B
IGS WA 3423/3412	44	29	32	11
WA 3307	31	22	23	-
WA 3416	40	-	-	-

Discussion. H. mintlyni is placed in the subgenus Hartwellia because tooth 1 is not situated close in between 3a and 3b as in H. (Tealbya) but is closer to the situation in H. (Hartwellia) although it does appear to be intermediate between H. H. hartwellensis and H. (Tealbya) tealbiensis. The hinge of H. (H.) groenlandica, from the Middle Volgian of East Greenland is similar, but the species is distinguished by having a more prominent and strongly prosogyrate umbonal region.

Externally some Hartwellia s.s may superficially resemble H. mintlyni however H. (H.) hartwellensis possesses a flatter nepionic shell

and bears more distinct posterior carina. H. (H.) kharoschovensis (Rouillier and Vossinsky) from the Middle Volgian of the Russian Platform may be distinguished by the neanic ornament which continues to a length of about 25 mm and then gives way gradually and not sharply to the later smoother adult ornament.

Subgenus

CLAXBYA subgen. nov.

Type Species. Cyprina claxbiensis Woods, (1907) pl. 20, fig. 1. Claxby Ironstone of Benniworth Haven, Lincs. Probably of Lower Valanginian age.

Diagnosis. Hartwelliid with reduced lateral teeth subhorizontal 3b and subtrapezoidal outline. Posterior area weakly demarcated.

Discussion. Hartwellia (Claxbya) is the second hartwelliid lineage which crosses the Jurassic-Cretaceous boundary. The type species, Cyprina claxbiensis Woods, was regarded by Casey (1952, p. 128) as Hartwellia s.s., however its distinctive dentition (Figure 3.13) and the trapezoidal outline distinguish it immediately from Hartwellia s.s. and Hartwellia (Tealbya). The subgenus can be traced back into the Middle Volgian where H. (C.) cancriniana (d'Orbigny) appears in the Hartwell Clay (IGS) of south central England and on the Russian Platform (Gerasimov 1955).

Occurrence Middle Volgian to Lower Valanginian of eastern England, Middle Volgian of the Russian Platform.

Hartwellia (Claxbya) cancriniana (d'Orbigny) 1845

Plate 23, figures 1a,b, 2; text figures 3, 12a, b

*1845 Cyprina cancriniana sp. nov. d'Orbigny, p. 457, pl. 38, figs. 26, 27

1845 Rouillier pl. E, fig. 8.

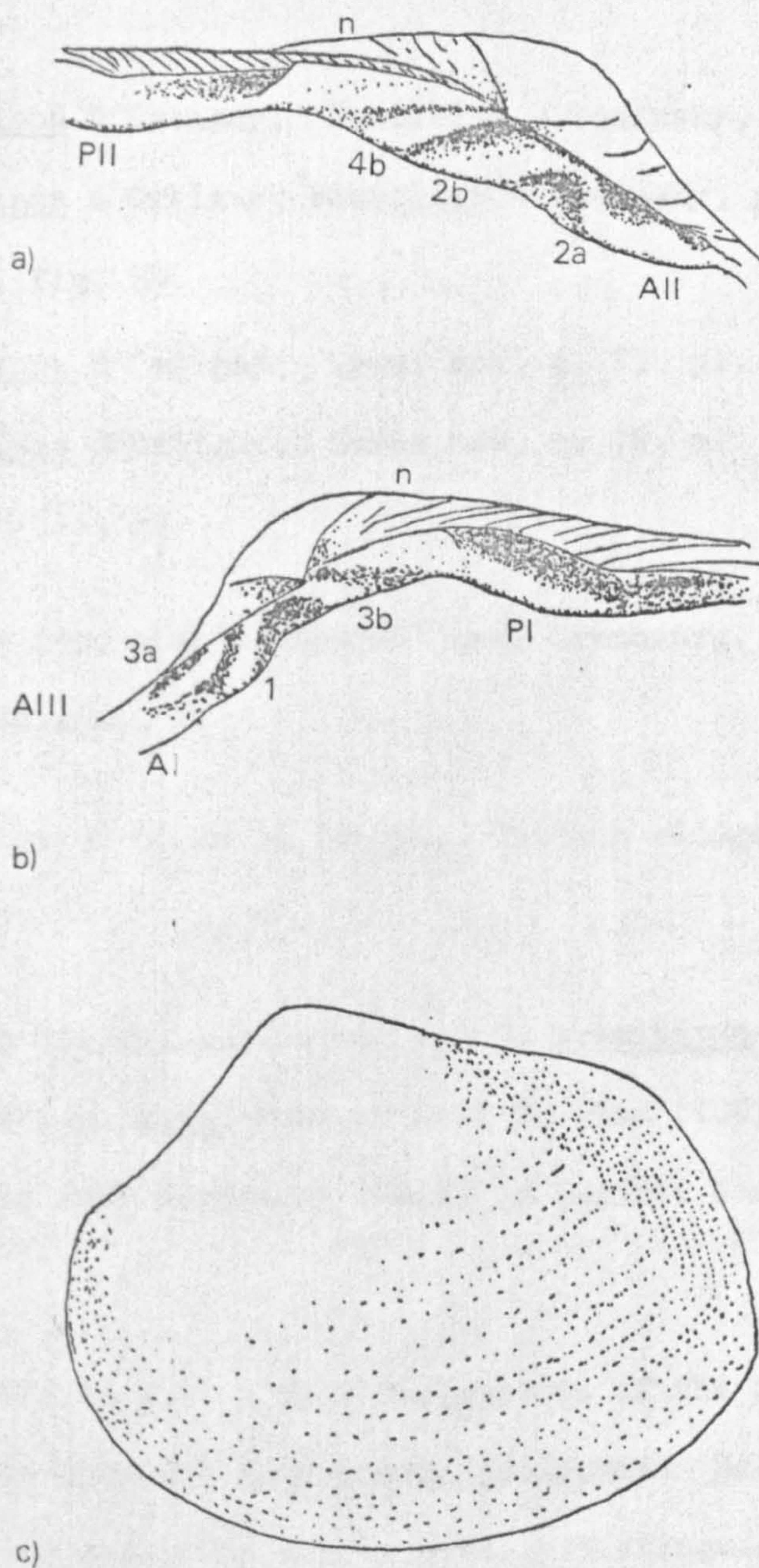


Figure 3.13

Figs. 13a-c. *Hartwellia* (*Claxbya*) *claxbiensis* (Woods) subgen. nov.
 a, SRAK JG.556, left valve hinge, 1.5m above base of Claxby Ironstone, Benniworth Haven Lincs; b, SRAK KY.1050, right valve hinge, basal conglomerate of Claxby Ironstone, Nettleton, Lincs; c, after Woods, 1907, pl. 21, fig. 2, left valve exterior, Benniworth Haven, Lincs. All xl.

- 1847 Cyprina cancriniana d'Orbigny; Rouillier & Vosinsky, p. 422
- 1848 Cyprina cancriniana d'Orbigny; Rouillier & Vosinsky, pp. 276-277.
286, pl. H, fig. 34.
- 1955 Cyprina cancriniana d'Orbigny; Gerasimov, p. 71, pl. 7, figs. 3, 4.
- 1969 Cyprina cancriniana d'Orbigny; Gerasimov, p. 76, pl. 4, fig. 12.
pl. 6, figs. 15, 17.

Types. Original material came from the 'Oxfordien' near Orenbourg. Untraced, believed lost. Age probably Volgian.

Diagnosis. Adult shell normally 40-60 mm in length. Outline elongate, trapezoidal.

Material. 4 specimens. Basal Spilsby nodule bed and S. primitivus Zone of Nettleton (SRAK); Mintlyn Beds, H. kochi Zone of West Dereham (IGS); and unhorizoned erratic block of Spilsby Sandstone (SRAK) in Leziate Sand Pit, Norfolk.

Discussion. It is not possible to give a full description of the species based upon Spilsby specimens as they are only poorly preserved. However isolated internal moulds lacking dentition may be readily distinguished from Hartwellia s.s. and Hartwellia (Tealbya) by the straighter ventral margin which parallels the posterodorsal margin, and by the posterior area which is relatively flat.

Occurrence. Middle Volgian of south central and eastern England and the Russian Platform. Upper Volgian to Ryazanian of eastern England.

Order	MYOIDA Stoliczka, 1870
Suborder	MYINA Stoliczka, 1870
Superfamily	GASTROCHAENACEA Gray, 1840
Family	GASTROCHAENIDAE Gray, 1840
Genus	GASTROCHAENA Spengler, 1783

Gastrochaena sp.

Plate 24, figs. 14, 15.

Discussion. One rock specimen is known (SRAK IG.2123) from the Basal Spilsby Nodule Bed, Nettleton, which contains two internal moulds of Gastrochaena within flask shaped borings in a phosphatised nodule. Also one external mould is visible and a cast of this is illustrated (Plate 24, figure 14). The specimens do not merit comparison with other gastrochaenids in the Upper Jurassic of north west Europe, but interest lies in the association of these Gastrochaena with Hiatella in borings in the same nodule bed. For discussion of this see Hiatella (Pseudosaxicava) foetida (Cox) and also the chapter on Paleoecology.

Superfamily	HIATELLACEA Gray, 1824
Family	HIATELLIDAE Gray, 1824
Genus	HIATELLA Bosc, 1801
Subgenus	PSEUDOSAXICAVA Chavan, 1952

Hiatella (Pseudosaxicava) foetida (Cox) 1929

Plate 24, figures 1-13, 16; plate 25, figures 1-8, plate 26, figures 1-3; text figure 3.14..

*vp. "Arca" foetida sp. nov. Cox, pp. 140-141, pl. 1, figs 2, 3.

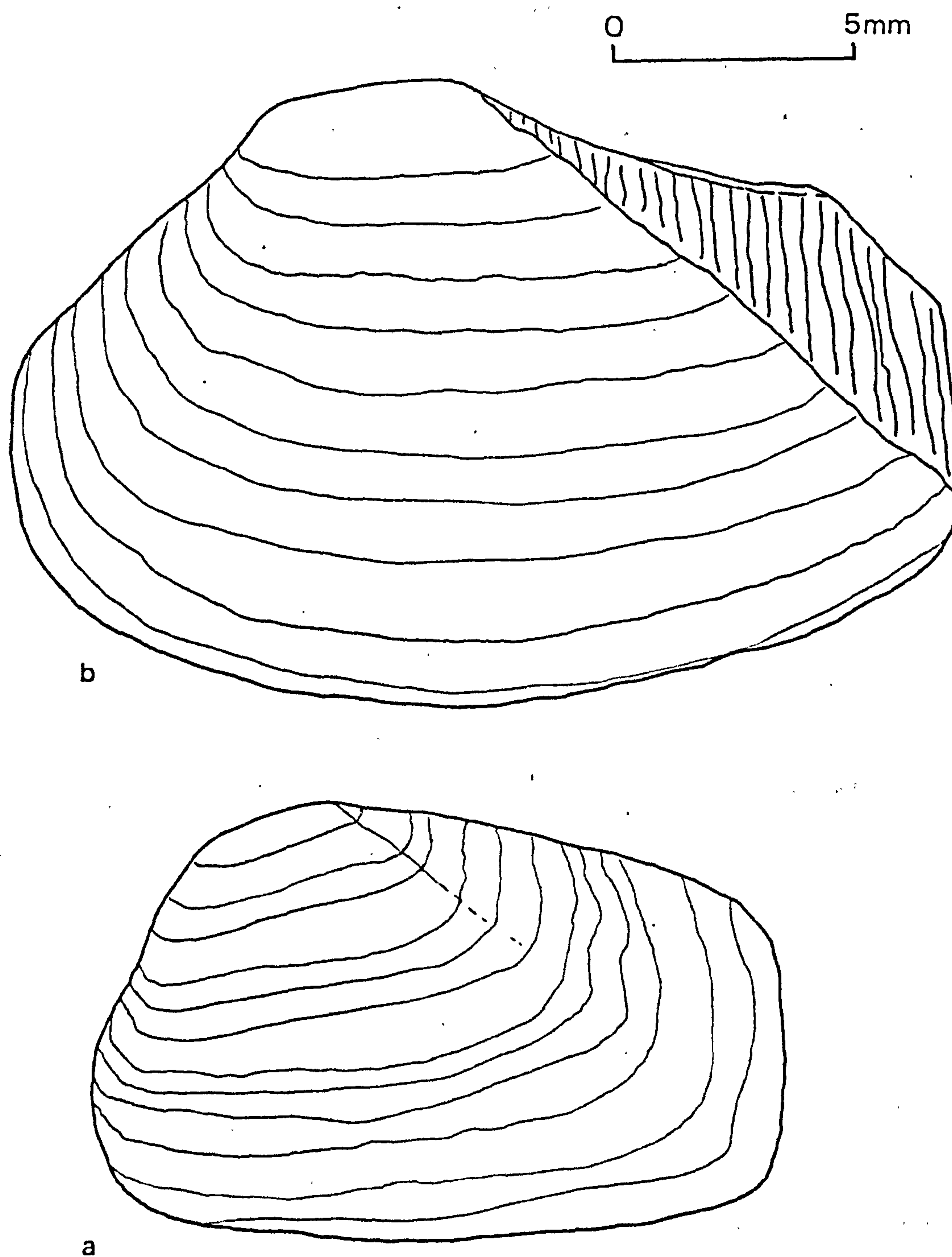


Figure 3.14

Sketch figures of Hiatella (Pseudosaxicava) foetida(Cox) showing, fig. a, typical form taken from boring and b, form that has not become constricted during growth. After specimens from the Basal Spilsby Nodule Bed, Nettleton, Lincs.

Types. Holotype: C.H. Waddington Collection, (Untraced), Portland Sands Hounstout, Dorset. Paratypes: specimens in Waddington Collection (information as for holotype), others including BMNH 34539 from the Hartwell Clay, Middle Volgian, of Buckinghamshire.

Diagnosis. Shell elongate, up to 29 mm in length, distinct posterior area in juveniles with posterior and escutcheon carinae. Hinge edentulous (?) with possibly one feeble tooth in each valve.

Material. 150 specimens. Abundant in the Basal Spilsby Nodule Bed of Nettleton, Lincs (SRAK). 6 specimens in the basal conglomerate of the Lower Greensand of Brickhill, Beds., (SMC). 1 specimen associated with Aulacostephanus, Kimmeridge Clay, Kimmeridgian, Swindon, Wilts (SRAK). Common in Hartwell Clay of Bucks (BMNH, IGS).

Description. The species embraces two ecologically controlled varieties in the Basal Spilsby Nodule Beds. It is first described in general terms before the two varieties are distinguished.

The shell is of small to medium size, elongate and trapezoidal in outline with maximum length 29 mm. The shell is thin and moderately inflated. The umbo is low and blunt and sited about one third to one quarter the length of the shell from the anterior. The beaks are small and prosogyrate. The shell anterior is evenly rounded. The ventral margin is straight to weakly concave. The posterior is truncate vertically but with rounded junctions with the ventral and dorsal margins. Posterodorsal margin is relatively straight. The shell surface is almost smooth, but bears fine irregular growth lines and also radial rows of minute pustules, similar to those on Pleuromya. There is a distinct posterior carina which

is weakly raised and runs to the posteroventral angle. The posterior area varies from being flat to either weakly concave or convex. It is ornamented by coarse irregular low lamellae. The dorsal margin of the posterior area is defined by a raised escutcheon carina which extends to the posterior margin. The escutcheon is narrowly lanceolate and there is a small external ligament. Internally the shell is smooth. The hinge is weak and appears to be edentulous though traces of a single cardinal tooth may be seen in each valve. The adductor scars and pallial line are obscure.

The two ecological varieties of Hiatella recognised here are as follows. The first is represented by relatively small individuals usually up to about 12 mm length which are normally found by cracking open flask shaped borings (Plate 24, figures 1-4, 6-8, 11). The second larger variety is normally found as internal moulds, usually up to about 29 mm length (Plate 24, figures 5, 9). The first variety is believed to have occupied the borings and may have been responsible for their construction. The second variety is believed to have been byssally attached to the exterior of the phosphatised nodules when exposed on the sea floor. Apart from the size difference the forms occupying the borings tend to lose the posterior and escutcheon carinae away from the umbo, the latest growth lines may be crowded and the posterior area ornament may be suppressed. In the epifaunally attached form, the posterior and escutcheon carinae are well formed throughout life together with the ornament on the posterior area and the flank is commonly concave in a manner similar to that in modiolids with a concave ventral margin. Material from the Kimmeridge Clay and Portland Sand is all the epifaunal variety.

Measurements.

	L	Lp	H	B
SRAK IR. 37	8	5	5	3
SRAK IG.1112	15	11	10	7
1617	18	13	12	7
2028	29	20	14	11
2286	11	7	9	5
2288	13	10	7	3'
2291	12	10	8	7
2298	17	12	11	8

Discussion. Although Cox (1929) originally referred this species to "Arca", it is quite clear that only the exterior with distinct posterior carina resembles an arcid. The lack of taxodont dentition and the presence of an escutcheon carina show that it has no relation with this group. H. (P.) bernardi (Chavan, 1952), from the Lower Kimmeridgian of Calvados, may be directly ancestral to H. foetida, but differs in having a more cuneiform shell with a relatively deeper posterior. In the Middle Jurassic of Calvados earlier examples of Hiatella (Pseudosaxicava) are recorded by Deslongchamps (1838) as Saxicava phaseolus Deslongchamps, a very elongate cylindrical form and S. dispar Deslongchamps, a form even more bluntly cuneiform than H. (P.) bernardi. These latter records appear to be the earliest of Hiatella.

The ecologically controlled varieties of Hiatella from the basal Spilsby Sandstone are paralleled almost exactly by recent hiatellids from the British Isles discussed by Hunter (1949). Hiatella gallicana (Lamarck) has the umbonal region and the posterior and escutcheon carinae worn from

living within flask shaped borings, while H. arctica (Linné) has clearly developed posterior and escutcheon carinae and often has a concave ventral margin and is normally found associated with byssate epifauna on rocks commonly together with mytilids.

The boring associated with Hiatella is flask shaped and unlined. The cross section of the neck and main body of the flask are rounded (Plate 26, fig. 3), while the aperture when not eroded is slightly oval (Plate 25, figure 1b). The borings commonly reach about 30 mm in length, with maximum diameter of about 13 mm and the neck about 5 mm. Although normally straight (Plate 25, figure 3), the necks may commonly be bent (Plate 25, figure 4,8). The substrate of the borings is a phosphatic nodule or conglomerate of such nodules, and as all the substrate appears to be equally lithified by phosphatisation the borings penetrate both clasts and matrix alike (Plate 24 figure 10, plate 26, figures 1, 3). Plate 25, figure 1 shows a large piece of bone, probably reptilean, which has been attacked by boring bivalves. The flask shaped cavities are seen in vertical section in figure 1a, with a specimen of Hiatella in situ. The outer surface of the bone has not been eroded since the bivalve attack was made and the weakly oval boring apertures are clearly seen in figure 1b. However in Plate 24, figure 16, the flask shaped cavities have been eroded away almost to their deepest point of penetration. The boring infillings are always phosphatised silty sand, and the coronas around some of the clasts indicate that several phases of phosphatisation have occurred in a manner similar to that described by Kennedy and Klinger (1972) in the Lower Cretaceous of southern Africa. The repeated phases of phosphatisation will also allow the development of interpenetrating borings as in Plate 25, figures 2, 6. Although it has

already been stated that Gastrochaena occurs rarely in the borings, the commonest occupant is Hiatella (Plate 25, figures 7, 8) and no trace has yet been seen of the calcareous linings present in some borings made by Gastrochaena borings. However only occasionally does the Hiatella shell completely fill the boring (Plate 24, figure 11) and it is common to find the occupant considerably smaller than the boring itself (Plate 26, figure 2), and also two or more individuals may occupy the same boring (Plate 24, figure 13; plate 25, figure 7). This would indicate that old borings are being reinfested by the pelagic larvae. When two shells occur in the same boring it is difficult to decide whether occupation was consecutive or contemporary. However all Hiatella found in borings have had the posterior of the shell pointing in the direction of the aperture of the boring, to allow clean water exchange through the siphons. It is not clear whether Hiatella has made these borings in the Basal Spilsby Nodule Bed, or whether the borings were originally made by Gastrochaena and the latter genus has almost completely disappeared. Certainly some of the borings have been reinfested by Hiatella as shown by the crowded growth lines on some small individuals, and the small size of others in comparison to the borings that they occupy. Hunter (1949) believes that modern Hiatella is capable of making borings in partly calcareous lithified substrates and non-calcareous substrates by a process of abrasion using mucus and rock fragments, but further work needs to be done on the process of boring.

The shape of the flask shaped boring (Plate 25, figures 2-8) in which Hiatella and Gastrochaena are found corresponds to the ichnogenus Gastrochaenolites Leymerie (1842, pp. 2-3, pl. 3, fig. 1), which was described in association with Gastrochaena dilatata Deshayes from the Calcaire à Spatangues, Neocomian, of the Aube, France. It was described

as a rock boring and has slightly sinuous sides unlike the wood boring Teredolites Leymerie (1842), from the same strata, which has evenly tapered sides and more truncate base to the flask. Bromley (1972) has placed both Teredolites and Gastrochaenolites within Trypanites Magdefrau (1952) which Häntzschel (1975, p. W136) restricts to straight tunnels with 1-2 mm width which are probably the result of polychaete activity. It is believed here that the ichnogenera Teredolites and Gastrochaenolites are similar but distinct borings made by bivalves and both names are valid.

Occurrence. Hiatella (Pseudosaxicava) foetida ranges from the Kimmeridgian to Middle Volgian of England.

Subclass	ANOMALODESMATA Dall, 1889
Order	PHOLADOMYOIDA Newell, 1965
Superfamily	PHOLADOMYACEA Gray, 1847
Family	PHOLADOMYIDAE Gray, 1847
Genus	GIRARDOTIA de Loriol, 1903

Discussion. The range of this genus should be extended into the Lower Cretaceous up to the Hauterivian of Europe.

Girardotia compressa (J. de C. Sowerby) 1829)

Plate 27, figures 1 a-c, 2, 3a, b, 4

- *.1829 Pholas? compressa sp. nov. J. de C. Sowerby, p. 216, pl. 603.
- .1868 Pholas Foucardi sp. nov. de Loriol, pp. 502-503, pl. 6, fig. 4.
- 1875 Pholas compressa Sowerby; Blake, pp. 214, 220.
- v.1888 Pholas compressa Sowerby; Morris and Lycett in Damon, pl. 15, fig.1.
- .1922 Pholadidea Fortini sp. nov. Cossman, p. 343, pl. 8, figs. 1-4.
- .1955 Girardotia suchanovens sp. nov. Gerasimov, pp. 87-88, pl. 15, fig. 1.

.1974 Girardotia aff. suchanovensis Gerasimov; Zakharov & Mesezhnikov
p. 158, pl. 36, figs. 3,4.

Types. The type material of J. de C. Sowerby, which came from the Kimmeridge Clay of Shotover, Oxfordshire, is untraced, believed lost. A neotype is therefore proposed IGS Y1558, from the Huddleston Collection from the same horizon and locality. It is figured on Plate 27, figure 1a-c. It is a composite mould from a calcareous concretion.

Diagnosis. Adult shell 30-40 mm in length. Coarse radial ornament on posterior. Fine radial ornament on the posterior half of anterior. Median groove in left valve only.

Material. 8 specimens (SRAK) from the Basal Spilsby Nodule Bed, Nettleton, Lincs.

Description. Shell small to medium size, strongly inflated and thin. Elongate in adults with maximum length c40 mm, although more lozenge shaped in juveniles. Umbones low with small orthogyrate beaks, situated about one third the length of the shell from the posterior. The posterior of the shell is evenly rounded with posteroventral margin obliquely truncate and terminating at the mid flank groove. Anterior somewhat produced in an anteroventral direction. The flank is divided by a broad sulcus which runs from the umbo in an anteroventral direction to the margin. In the left valve this centres on a radial groove which is not present on the right valve. The posterior part of the posterior of the flank is ornamented by about 8 widely spaced ribs and to the anterior of these are a further c10 closely set ribs. The posterior of the anterior half of the flank is ornamented by about 15 closely set radial ribs, but the antero-dorsal part has no radial ornament.

Superimposed on the whole flank are regular widely spaced commarginal raised lamellae up to 2 mm apart. On internal moulds the coarser radial ribs and part of the commarginal ornament are reflected, otherwise it is smooth. Details of the hinge and musculature are obscure. The valves gape strongly at both the anterior and posterior and are only in contact along the hinge, at the beak and at the most ventral part of the flank.

Dimensions

	L	H	Lp	B
Holotype IGS Y1558	40	23	24	20
SRAK IG.2116	30	21	21	9
3123	27	15	17	6

Discussion. Although G. compressa is relatively common in the Lower Kimmeridge Clay of southern England, it is otherwise scarce and is not figured in accessible literature and consequently overlooked in recent publications. All the specimens included in the synonymy above come from the Kimmeridgian to Middle Volgian.

Early records of G. compressa in England include the occurrence of the species in the lowermost Kimmeridge Clay of Weymouth (Blake 1875; Morris and Lycett in Damon 1888): In France the species was first recognised as Pholas Foucardi de Loriol (1868) from the 'Zone a Pinna suprajurensis' of the Yonne. The figured individual is only about 12 mm in length and is an internal mould, consequently there is little trace of the external ornament. It resembles closely a smaller version of the specimen figured on plate 27, figure 2. The specimens labelled Pholadidea Fortini Cossman (1922) from the Portlandien moyen of Rouen shows more clearly the features of Girardotia. Although the lateral profile appears more wedge shaped and

the umbo closer to the posterior than in the specimens figured here, I am satisfied that they belong within the same species. G. suchanovensis Gerasimov (1955) from the Middle Volgian of the Russian Platform shows an incomplete internal mould of a right valve, very similar again to plate 27, figure 2, but showing slightly more distinct commarginal ornament.

G. aff suchanovensis from the Lower Volgian of the North Urals figured by Zakharov and Mesezhnikov (1974) is again an internal mould but which also shows traces of the finer radial ornament.

G. pulchella Rollier (1913, 1914), from the Upper Oxfordian of the Jura Bernois may have a radial groove in both valves and therefore be distinct from G. compressa, but other features are broadly similar. The type species, G. elegans de Loriol (1903) from the French Argovian, is larger than G. compressa and bears much finer radial ornament. G. wrighti sp. nov., described below, is also larger but bears virtually no radial ornament. G. koeneni (Wollemann 1900) from the Neocomian of north Germany, although generally similar to G. compressa, has radial ornament only as coarse ribs on the very posterior of the shell.

Occurrence. Lower Kimmeridgian to Middle Volgian of England; Lower Volgian of northern and eastern France; Middle Volgian of the Russian Platform; Lower Volgian of the North Urals.

Girardotia wrighti sp. nov.

Plate 27, figures 5-8.

Types. Holotype: Wright Collection, BMNH 4795, matrix of fine limonitic oololiths in buff limestone, presumed to be a limestone low in the Lower Tealby Clay (fide Rawson pers. comm.), Hauterivian, of Nettleton, Lincs.

5 paratypes: GSM B.D.F. 4825, Lower Tealby Clay, Hauterivian, Skegness Borehole (1970), Lincs.; Lamplugh Collection, BMNH L. 60037 and Rhodes Collection, IGS R.27/96 both from the Hundleby Clay, Valanginian, Hundleby Brickyard, Lincs. IGS CE4660, Mintlyn Beds, S. stenomphalus Zone, Ryazanian, King's Lynn Bypass, Norfolk; IGS WA3206/3207, Mintlyn Beds, H. kochi Zone Ryazanian, Flood Relief Channel, West Dereham, Norfolk.

Diagnosis. Adult shell large and deep. External ornament of commarginal raised lamellae; radial elements restricted to feeble development of coarse posterior ribs.

Description. Adult shell large, usually 60-75 mm in length, inflated and thin. Lateral outline elongate lozenge shaped, with low umbo and small beaks located just posterior to the mid line. Posterior deep and rounded, anterior shallower and more produced. The valves gape strongly at the anterior and the posterior, and are only in contact at the hinge line and beaks and at a point at the most distal part of the mid-flank sulcus. The flank is divided by the broad umbonoventral sulcus which is less conspicuous in the right valve and in the left valve is centred on a distinct groove. The flank ornament is composed of regular raised commarginal lamellae spaced about 2-4 mm apart. Radial ribs are not developed except that feeble traces of the coarse radial ribs may be seen as slightly lamellose tubercles on the commarginal lamellae. (Plate 27, figure 5). Internally the shell is smooth, but the commarginal ornament is represented by gentle folds. The hinge line is thickened to the posterior of the beaks, and there are traces of a further thickened slightly opisthocline rib immediately below (see Plate 27, figure 8c). The hinge appears to be edentulous but there may be traces of a single cardinal tooth in each valve.

Measurements.

	L	Lp	H	B
BMNH 4795	55+	29	43	32
IGS R27/96	65+	30	48	38
CE	75+	28	43	34

Discussion. G. wrighti is distinguished from species of similar age by its large size and lack of radial ornament. (See also discussion of G. compressa)

Genus GONIOMYA Agassiz, 1841

Goniomya (Goniomya) rawsoni sp. nov.

Plate 23, figure 10.

- .1936 Goniomya aff. sulcata Agassiz; Spath, pp. 129-130, pl. 44, fig. 1.
.1974 Goniomya cf. dubois Agassiz; Zakharov & Mesezhnikov, p. 157,
pl. 35, fig. 3.

Types. Holotype: IGS Bb4411, Swinnerton Collection, Top bed of Bed D, Lower Spilsby Sandstone 239½' below surface, S. primitivus Zone, Upper Volgian Fordington Well, Lincs. Paratypes: IHGPC, specimen illustrated by Spath 1936, pl. 44, fig. 1, probably Lingula Bed, Middle Volgian, Milne Land, East Greenland; Museum of the Institute of Geology and Geophysics, SO AN USSR No. 438/57, Middle Volgian, R. Yatria, N. Urals.

Diagnosis. Adult shell large and elongate. Ornament of chevrons without horizontal bar. Posterodorsal margin concave.

Description. (Based principally on the holotype, but with further

information based on the figures of Spath (1936) and Zakharov & Mesezhnikov (1974)). The holotype is large with length about 130 mm. The valves are in occlusion but crushed. The umbones and beaks are small projecting slightly above the hinge line. The posterodorsal margin is concave and the posterior margin is weakly inflated but obliquely truncate. The ventral margin is straight to slightly convex. The anterior margin is short and rounded. The flank is ornamented by coarse chevron shaped ribs which appear to die out in the more distal parts of the large specimens. The closure of the chevrons is v-shaped without a horizontal bar, and becomes slightly swept forward with distance from the umbo.

Discussion. Small specimens from the Mintlyn Beds of Norfolk are named Goniomya sp. juv. cf. rawsoni, as they correspond to the juvenile parts of the adult shells in the above description, but without the adults some doubt remains concerning the precise identification. The angulature of the ribbing is clearly shown sweeping forward (Plate 23, figures 8, 9).

Large Goniomya from the Corallian of Yorkshire has been referred to G. sulcata Agassiz by Arkell (1934). The species does not appear to reach as large a size as G. rawsoni, and the posterior appears to be more flared and rounded. In the Upper Jurassic of north west Europe the normal Goniomya is G. literata (J. Sowerby 1819) which is smaller with more symmetrical and prominent umbones. In this species a horizontal bar may be present or absent connecting the chevron ribs. G. dubois Agassiz (1842) may be a synonym of G. literata and is commonly recorded from the Upper Jurassic of eastern Europe and Russia.

Occurrence. Middle Volgian of eastern England, East Greenland and the North Urals. Possibly extending into the Ryazanian of eastern England.

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Occurrence. Middle Volgian of eastern England, East Greenland and the North Urals. Possibly extending into the Ryazanian of eastern England.

Chapter 4, PALEOECOLOGY

1. Introduction

The importance of bivalves as environmental indicators cannot be overstressed. In the fossil record they usually dominate the post Palaeozoic macrofaunal benthonic element of shallow shelf marine sediments. They have penetrated most aqueous environments and as a group are euryhaline but as individuals are normally stenohaline. Although the larvae are pelagic, bivalve adults are primarily benthonic. Their distribution is controlled by particular sedimentary requirements, temperature, depth, salinity, turbidity, currents, food supply, oxygenation, and predation.

Because modern counterparts of many of the fossil groups of bivalves exist today, they can be used extensively for comparison with the fossil forms. 100% of the Spilsby bivalve superfamilies, 67% of the families and 24% of the genera are living today. Recent forms are therefore the key to interpretation of the Spilsby bivalves. One publication has been of exceptional importance in this respect, it is the Relation of Shell Form to Life Habits of the Bivalvia by S. M. Stanley (1970).

The ecological significance of bivalves is still in a state of rapid expansion and exploration. Trophic analysis forms an important part of the study of ancient communities (Turpaeva, 1948; Walker 1972). Stanley (1968, 1970, 1972) has made very important contributions to the knowledge of functional morphology in both recent and fossil bivalves. Using this and other information, Mesozoic bivalve dominated assemblages have been studied by various authors including Rhoads, Speden and Waage (1972), Wright (1974) and Duff (1975). Hallam (1976) has attempted a broad synthesis of

Jurassic bivalve ecological associations in western Europe though detailed studies in most areas are still lacking. The Spilsby bivalves clearly fall into Hallam's nearshore marine association.

In this study, the bivalves are first examined briefly from an autecological point of view, that is the study of the life habits of an individual taxon in isolation. Secondly the synecology of selected levels in the Spilsby Sandstone and Sandringham Sands are examined, with particular emphasis upon those bivalves which dominate the benthonic biota. The palaeontologist can only work upon a visible assemblage and must take into account various factors including taphonomy, diagenesis and the problems of collecting before making an overall interpretation. Although the fossil assemblage cannot compare in the completeness to the original community, it is the closest that can be attained. Together with other palaeontological, sedimentological and stratigraphic studies of adjacent areas, an overall environmental picture and its evolution may be envisaged.

2. Palaeoautecology

The palaeoautecology of the Spilsby bivalvia is based partly upon whether the shell is found in life position eg. in a burrow or boring or cemented to a hard substrate and largely upon functional morphology of specimens that because of post mortal reorientation are no longer in life position. The shell shape and areas of attachment of soft parts are important keys to interpretation of the original life habits (Kauffman in Moore Ed. 1969; Stanley, 1970).

The autecology of the Spilsby bivalvia is summarised in figure 4.1. Because of the many parallel functions in the bivalvia it is possible to

Taxa	Life habit/ feeding group	EPIFAUNA				SEMI- INFAUNA	INFAUNA					
		Free swimming	Byssally nestling	Byssally pendant	Cemented	Byssally attached	Deposit feeder	Integripalliate	Weakly sinupalliate	Strongly sinupalliate	Mucus tube feeder	Rock Borer
'Nucula'							x					
Barbatia			x									
Grammatodon			x									
Cucullaea								x				
Musculus			x									
Lithophaga												x
Modiolus			x			x						
Falciomytilus			x									
Pinna						x						
Inoceramidae			x									
Isognomonidae			x									
Oxytoma				x								
Arctotis				x								
Entolium		x										
Camptonectes s.s.			x									
C. (Boreionectes)		x	x									
Buchia			x									
Plicatula					x							
Placunopsis					x							
Limidae			x									
Ostreacea					x							
Trigonidae								x				
Lucinidae								x			x	
Myoconcha						x?						
N. (Lyapinella)									x			
N. (Pressastarte)								x				
Nicaniella s.s.								x				
N. (Trautscholdia)								x				
Protocardia									x			
Senis										x		
Tellinidae										x		
Sowerbya										x		
Tancredia										x		
Corbicellopsis									x			
Anisocardia								x?				
Eartwellia									x			
Procyprina								x?				
Gastrochaena												x
Hiatella - boring											x?	x
Hiatella non boring		x										
Martesia												x
Pholadomyacea										x		
Girardotia										x	x	
Thracia										x	x	

Figure 4.1

Summary of the life habits and feeding groups of the Spilsby Bivalve fauna after Kauffman (in Moore Ed. 1969, p. N.141) and Duff (1975, p. 447).

unite several taxa into small groups depending on their principal feeding group and mode of life. This arrangement follows Kauffman (in Moore Ed. 1969) and Duff (1975). Elaborate discussion of the palaeoautecology of each taxon is avoided in order to save space. However the functional morphology of two species is discussed in some detail in the systematic descriptions of Hiatella foetida (Cox) and Camptonectes (Boreionectes) cinctus (J. Sowerby) in chapter 3.

3. Synecology.

The synecology is an attempt to reconstruct a picture of the overall environment using as many taxa as possible (bivalves and others) for each bed. The bivalves generally occupy over ninety percent of each assemblage. As the assemblages only partially represent the original community, some problems in assessing what remains or has been added to the assemblage are considered first. Five assemblages are recognised in the Spilsby Basin, all of which are dominated by bivalves. These enable one to obtain a picture of the original environment. The assemblages are used to produce a model of the biofacies evolution of the Spilsby Basin from Middle Volgian to Ryazanian times and this in turn is used with published information from surrounding areas to build up a palaeobiogeographical reconstruction of southern and eastern England during these times.

3a. Problems

In a recent study of the paleoecology of the Lower Oxford Clay, Duff (1975) was able to examine four continuous fossiliferous sections in actively worked clay pits. The preservation of the faunas was good with

aragonite shells frequently occurring. In the Spilsby basin information is much more difficult to collect from the many isolated horizons and localities. It is only from particular lithified horizons that any fauna can be collected. The bulk of the Spilsby Sandstone proper is unlithified and lacks sedimentary structures due to bioturbation. When fossils are found the aragonite is absent completely and calcitic fossils are only sometimes preserved. The bulk of the fauna is therefore collected in the form of moulds in calcareous, phosphatic and sideritic clay ironstone concretions (See "preservation" in chapter 3). It has been possible to utilise only 10 horizons for quantitative analysis of the assemblages and only 3 of these have been collected in bulk by the author. The others are represented by the collections of the IGS which approach bulk collections as near as possible. Most of the latter collections are preserved as rich faunas in blocks from which reasonable faunal counts were made. The numbers of specimens of each taxon collected at each horizon are listed fully in Appendix 6. The preservation of the fauna principally as moulds makes the process of accurately measuring specimens for population analysis both time consuming and costly and so has necessarily been avoided.

It is believed that the fresh nature of most moulds and the generally complete valves indicate that the assemblages are broadly life assemblages. However the epifaunal suspension feeders and shallow burrowing infauna frequently show signs of disarticulation due to burrowing and current rearrangement. The degree to which these processes have taken place will always be arguable, but it is believed here that generally transport has been over short distances and that faunas are still largely near their original life position.

	1 Basal Spilsby Nodule Bed, M. Volgian, Nettleton.	2 P. oppressus Zone concs. M. Volgian, Leziate.	3 S. preplicomphalus Zone U. Volgian, West Keal.	4 S. lamplughii Zone concs. U. Volgian, Nettleton.	5 S. lamplughii Zone nodules, U. Volgian, West Dereham	6 Basal Cretaceous Nodule Bed, Ryazanian, West Winch	7 Basal Cretaceous Nodule Bed, Ryazanian, North Runcton	8 Basal H. kochi Zone nodules, Ryazanian, West Dereham.	9 H. kochi Zone clay ironstone, Ryazanian, West Dereham	10 S. stenomphalus clay ironstn. Ryazanian, Mintlyn Wood.
<u>Whole Benthos.</u>										
Number of taxa	42	27	26	15	17	17	11	4	21	18
Number of individuals	1318	253	559	116	383	289	77	147	491	1992
No. in Trophic Nucleus	13	9	12	6	5	4	6	2	4	3
Diversity Index	13.5	11.2	9.4	7.3	6.6	6.9	5.8	2.3	7.8	5.5
Rank of Diversity Index	1	2	3	5	7	6	8	10	4	9
Rank from rarefaction curve	1	2	3	5	6	7	8	10	4	9
<u>Bivalve Fauna only.</u>										
Free Swimming %	0.95	32.72	61.27	60.71	0.79	0.37	7.79	57.82	2.30	0.10
Byssate	29.30	15.67	3.64	9.82	1.85	0.37	1.30	0.68	1.25	50.55
Cemented	13.40	9.22	0.18	1.79	-	-	-	-	-	0.25
Deposit Feeders	-	-	-	-	-	-	-	-	0.63	-
Integripalliate	16.08	20.74	13.64	4.46	30.42	10.44	16.88	41.50	15.45	0.75
Weakly Sinupalliate	2.25	8.75	5.27	11.61	55.82	78.73	63.63	-	64.09	45.38
Strongly Sinupalliate	25.50	3.68	12.18	8.04	7.14	10.07	10.34	0.68	13.78	1.41
Mucus tube feeders	11.84	9.22	3.64	3.57	2.38	-	-	-	2.30	0.10
Borers	0.69	-	-	-	1.59	-	-	-	0.21	1.41
<u>Major Life Habit/Function, with Free Swimmers.*</u>										
Epifauna	43.65	56.36	65.09	72.32	2.64	0.74	9.09	58.50	3.55	0.95
Infauna	56.36	42.39	34.63	27.68	97.35	99.24	90.85	42.13	95.83	99.04
Deposit Feeders	-	-	-	-	-	-	-	-	0.63	-
<u>Major Life Habit/Function, without Free Swimmers.*</u>										
Epifauna	43.11	36.99	9.86	29.55	1.86	0.37	1.41	1.61	1.28	0.95
Infauna	56.90	63.00	89.67	70.45	98.13	99.60	98.52	98.39	98.19	99.09
Deposit Feeders	-	-	-	-	-	-	-	-	0.64	-
* <u>Corbula</u> plots as infauna and <u>Hiatella</u> plots as epifauna.										

Figure 4.2

Comparative table of composition of 10 Spilsby Sandstone and Sandringham Sands assemblages.

Reworked phosphatised horizons should be treated with some caution as several horizons may be condensed into one. Selective preservation of parts of the fauna by phosphatisation may occur and affect only that part of the fauna which is buried. This preservation is discussed in the assemblages in which it occurs.

3b. Description of the assemblages.

Duff (1975) in his study of the Lower Oxford Clay faunas used triangular plots, rarefaction curves, trophic nuclei, trophic group composition and Diversity Index to examine whole benthonic assemblages. (See Duff, 1975, for definition of terminology). His system is largely followed here but is modified slightly. The trophic nuclei and faunal diversity are deduced from the whole benthonic fauna, while the Trophic Group composition is obtained from the bivalves only as it has not yet been possible to examine the life habits in minor groups like the gastropods. As bivalves generally comprise over 90% of the whole benthonic faunal assemblage this latter generalisation still gives a realistic figure.

The five bivalve dominated assemblages recognised here are:

1. Pleuromya/Grammatodon
2. Entolium
3. Lyapinella
4. Protocardia
5. Corbula

3b. Pleuromya-Grammatodon assemblage (Fig. 4.3a, b)

The assemblage has only been studied fully at Nettleton where

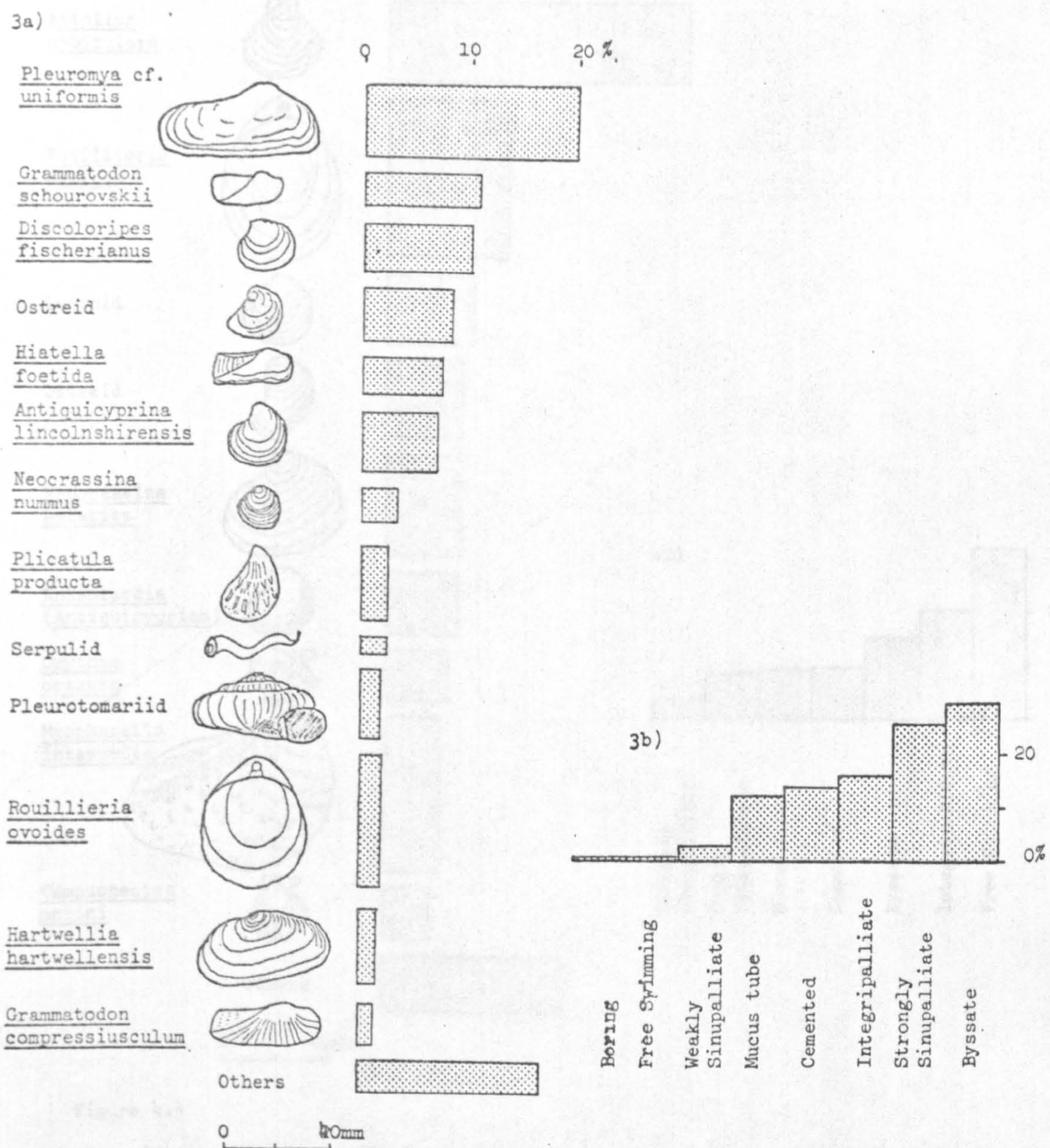


Figure 4.3

Composition of benthonic assemblage from the Basal Spilsby Nodule Bed, Middle Volgian, Nettleton Lincs. 3a, trophic nucleus (based on whole fauna). 3b, ranked distribution of principal life habit/feeding group composition (based on bivalves only).

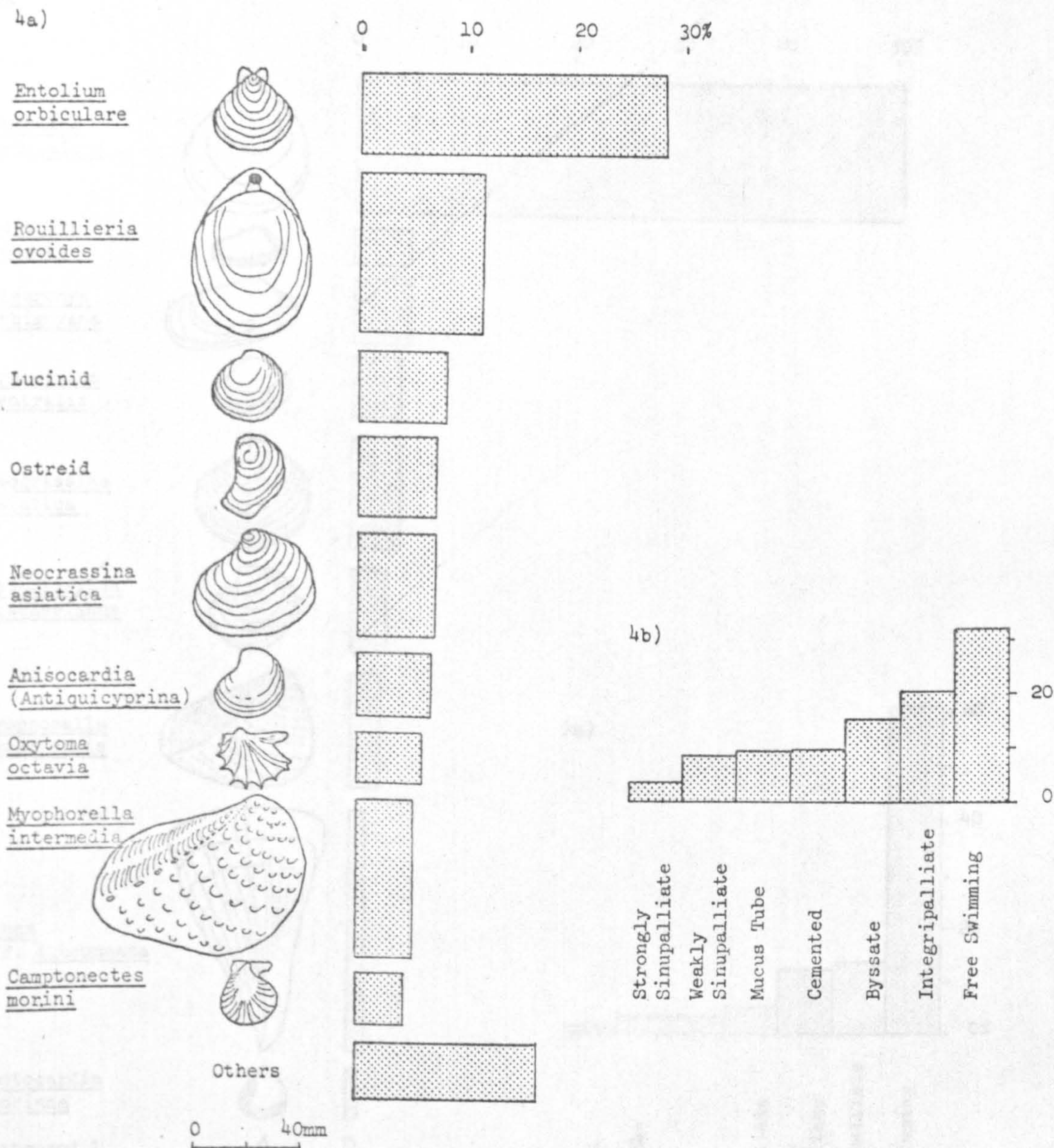
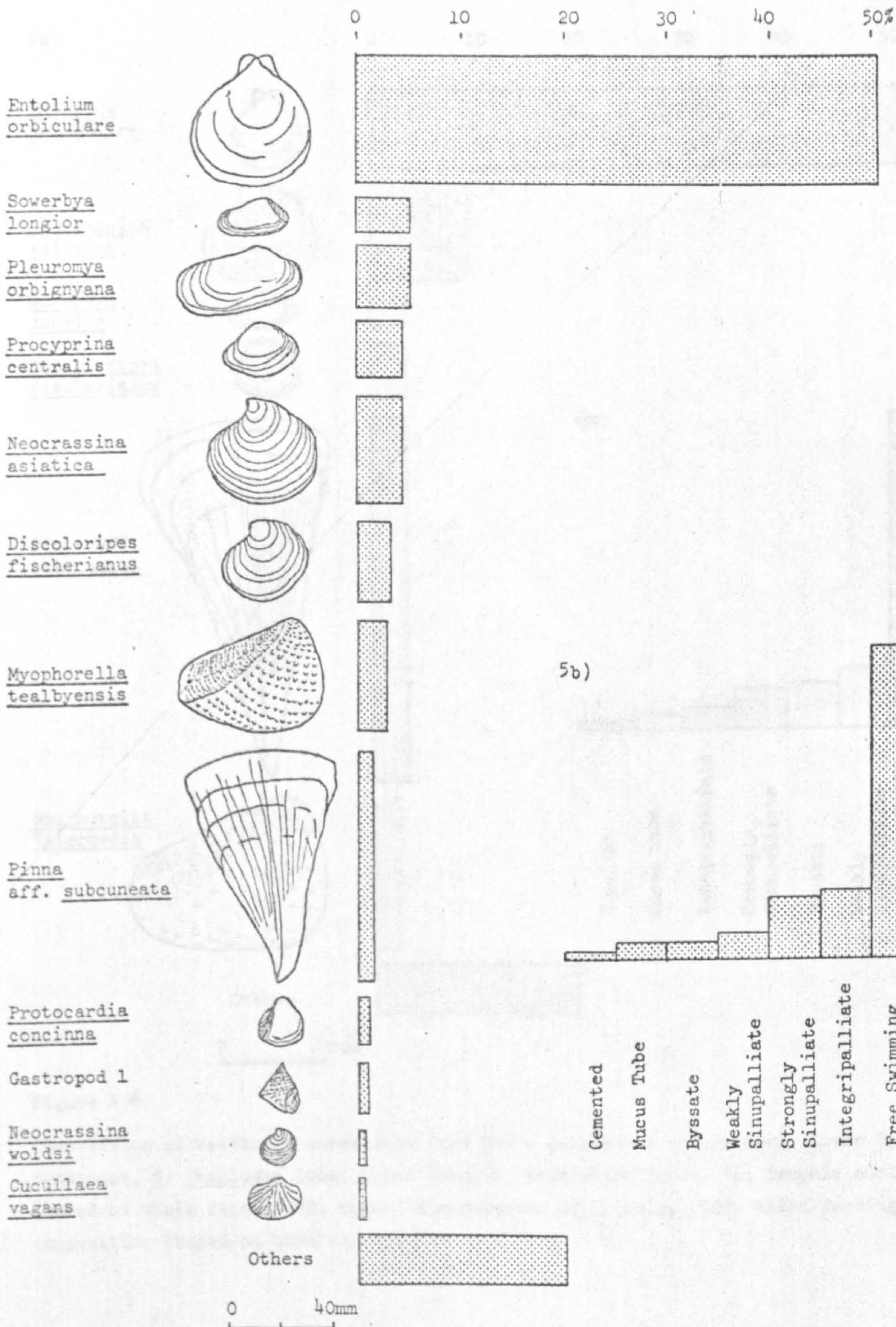


Figure 4.4

Composition of benthonic assemblage from erratic blocks of Lower Spilsby Sandstone, *P. oppressus* Zone, Middle Volgian, Leziate, Norfolk. 4a, trophic nucleus (based on whole fauna). 4b, ranked distribution of principal life habit/feeding group composition (based on bivalves only).

5a)



5b)

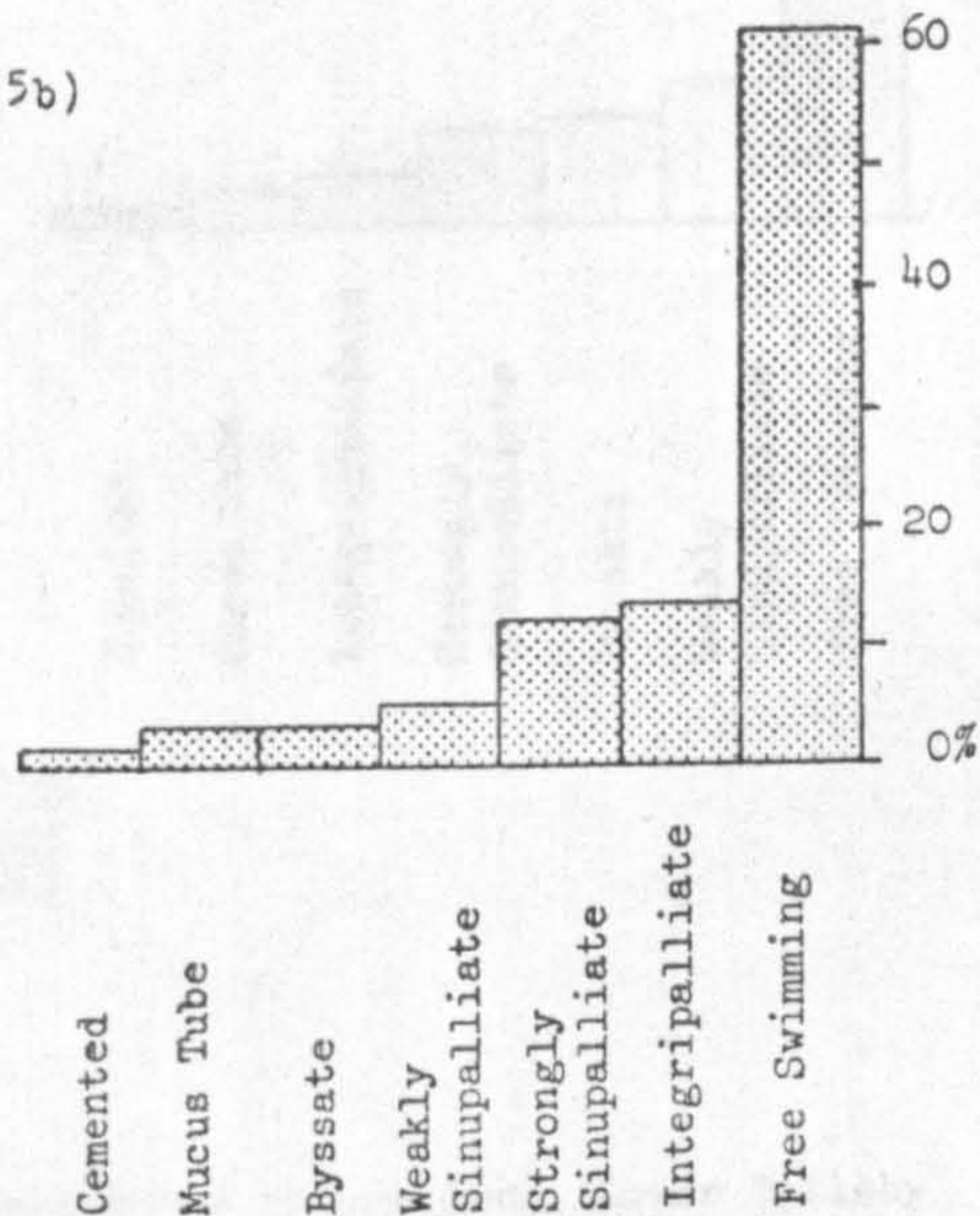


Figure 4.5

Composition of benthonic assemblage from Bed 1 calcareous concretions, Lower Spilsby Sandstone, *S. preplicomphalus* Zone, Upper Volgian, High Barn, West Keal, Lincs. 5a, trophic nucleus (based on whole fauna). 5b, ranked distribution of principal life habit/feeding group composition (based on bivalves only).

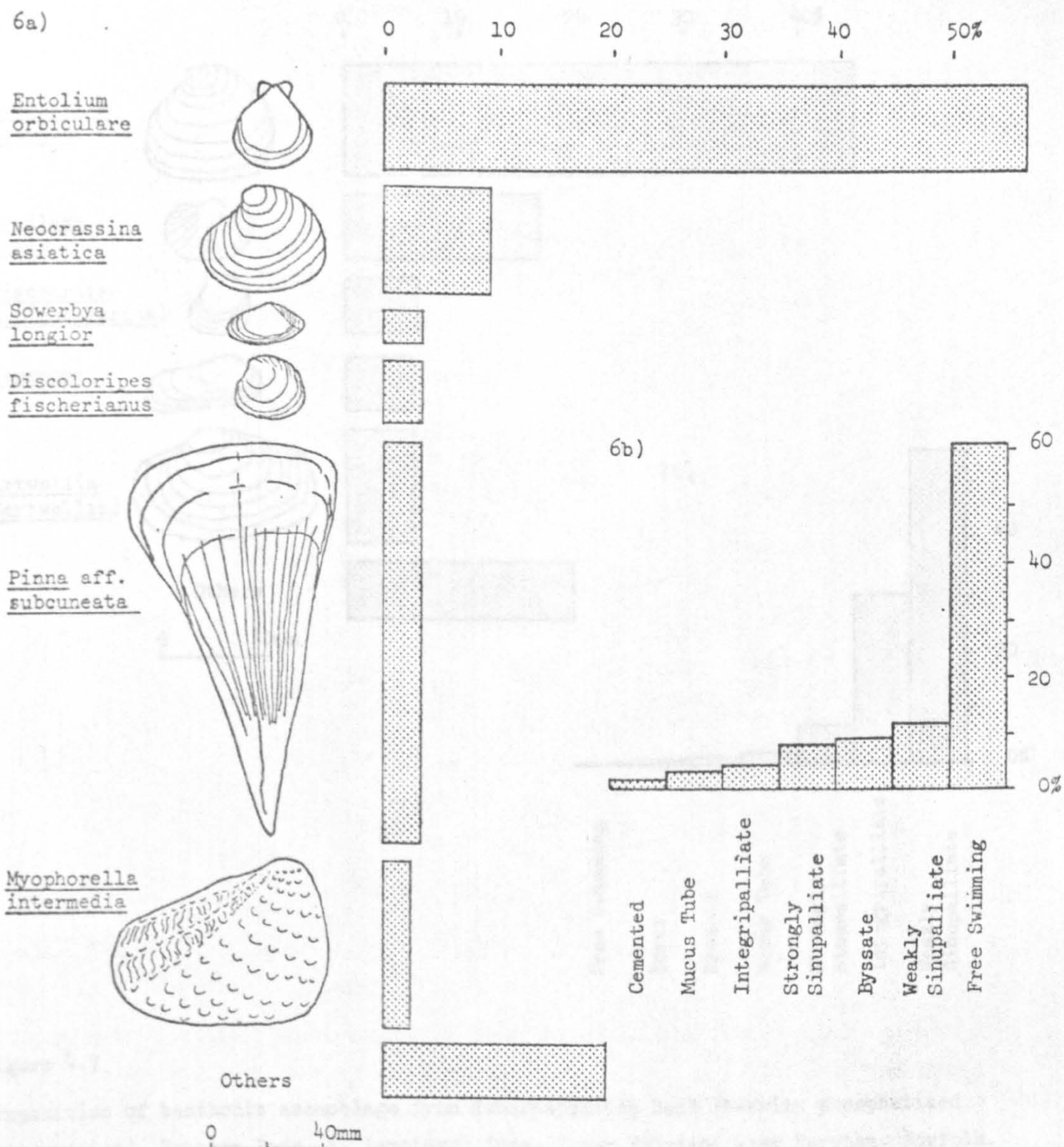


Figure 4.6

Composition of benthonic assemblage from Bed 6 calcareous concretions, Lower Spilsby Sandstone, *S. lamplughii* Zone, Upper Volgian, Nettleton, Lincs. 6a, trophic nucleus (based on whole fauna). 6b, ranked distribution of principal life habit/feeding group composition (based on bivalves only).

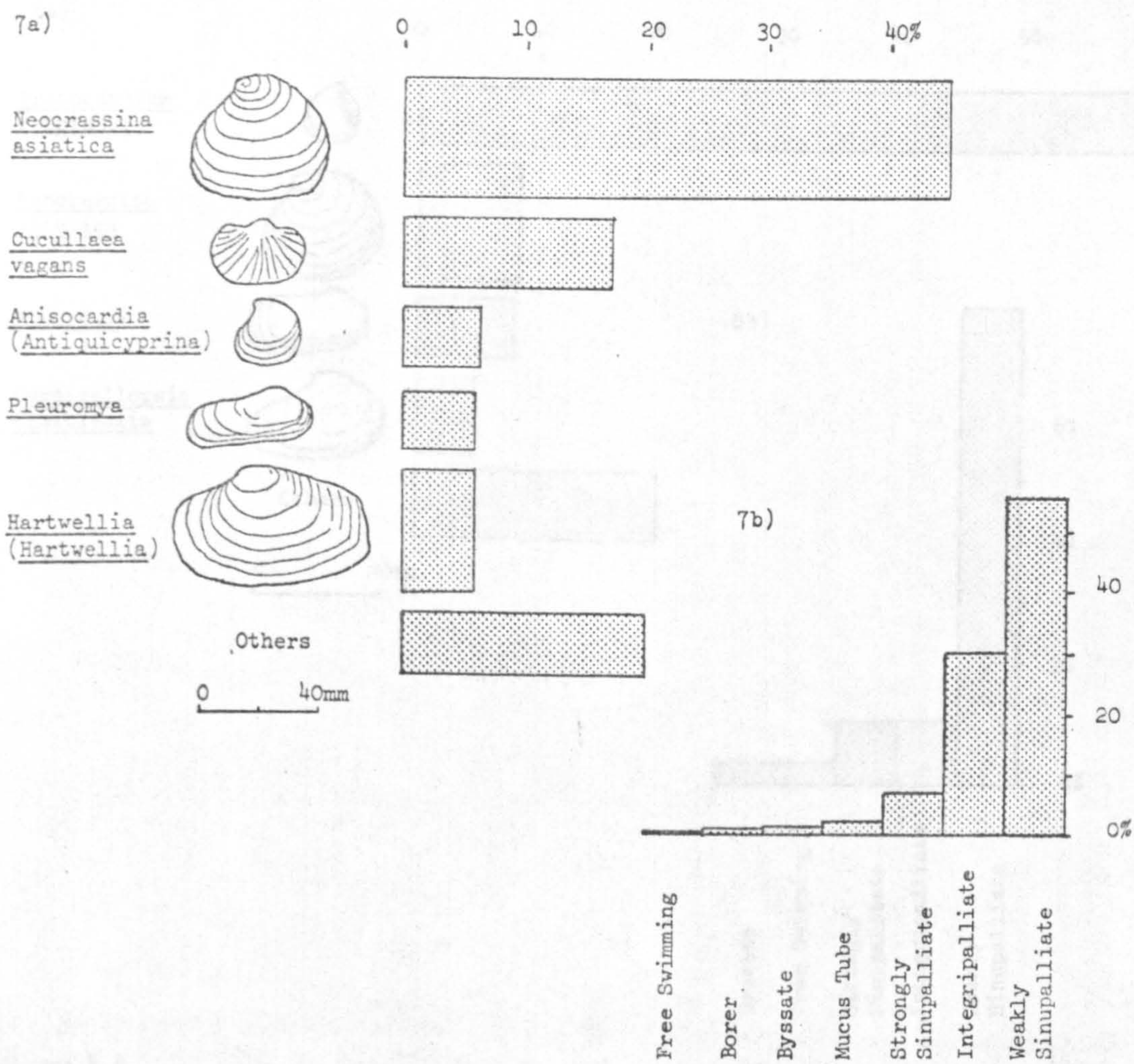


Figure 4.7

Composition of benthonic assemblage from Subcraspedites Band (heavily phosphatised preservation), Runceton Beds, *S. lamplughii* Zone, Upper Volgian, West Dereham, Norfolk. 7a, trophic nucleus (based on whole fauna). 7b, ranked distribution of principal life habit/feeding group composition (based on bivalves only).

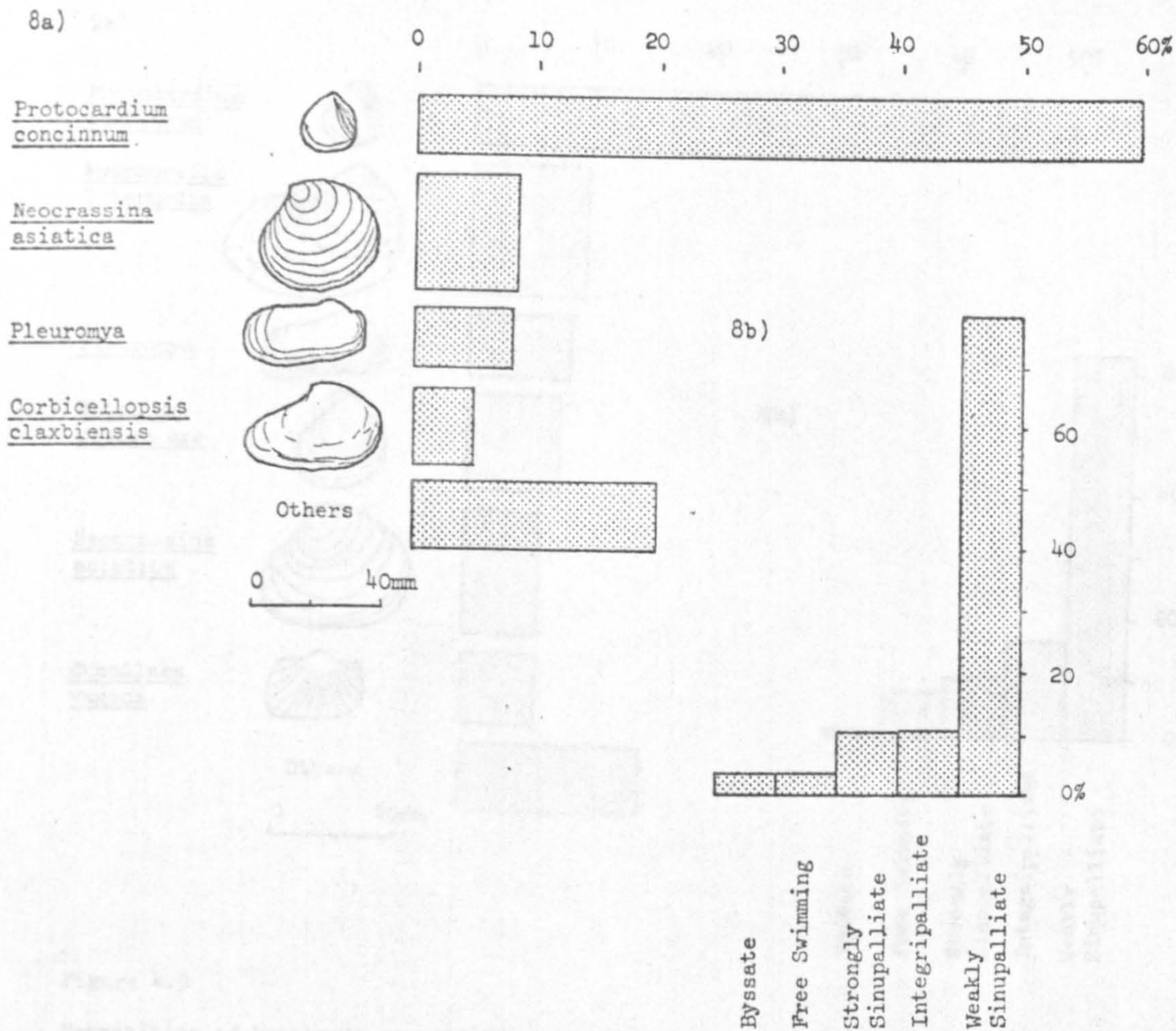


Figure 4.8. Composition of benthonic assemblage from Basal Mintlyn Nodule Bed, Ryazanian, West Winch, Norfolk. 8a, trophic nucleus (based on whole fauna). 8b, ranked distribution of principal life habit/feeding group composition (based on the bivalves only).

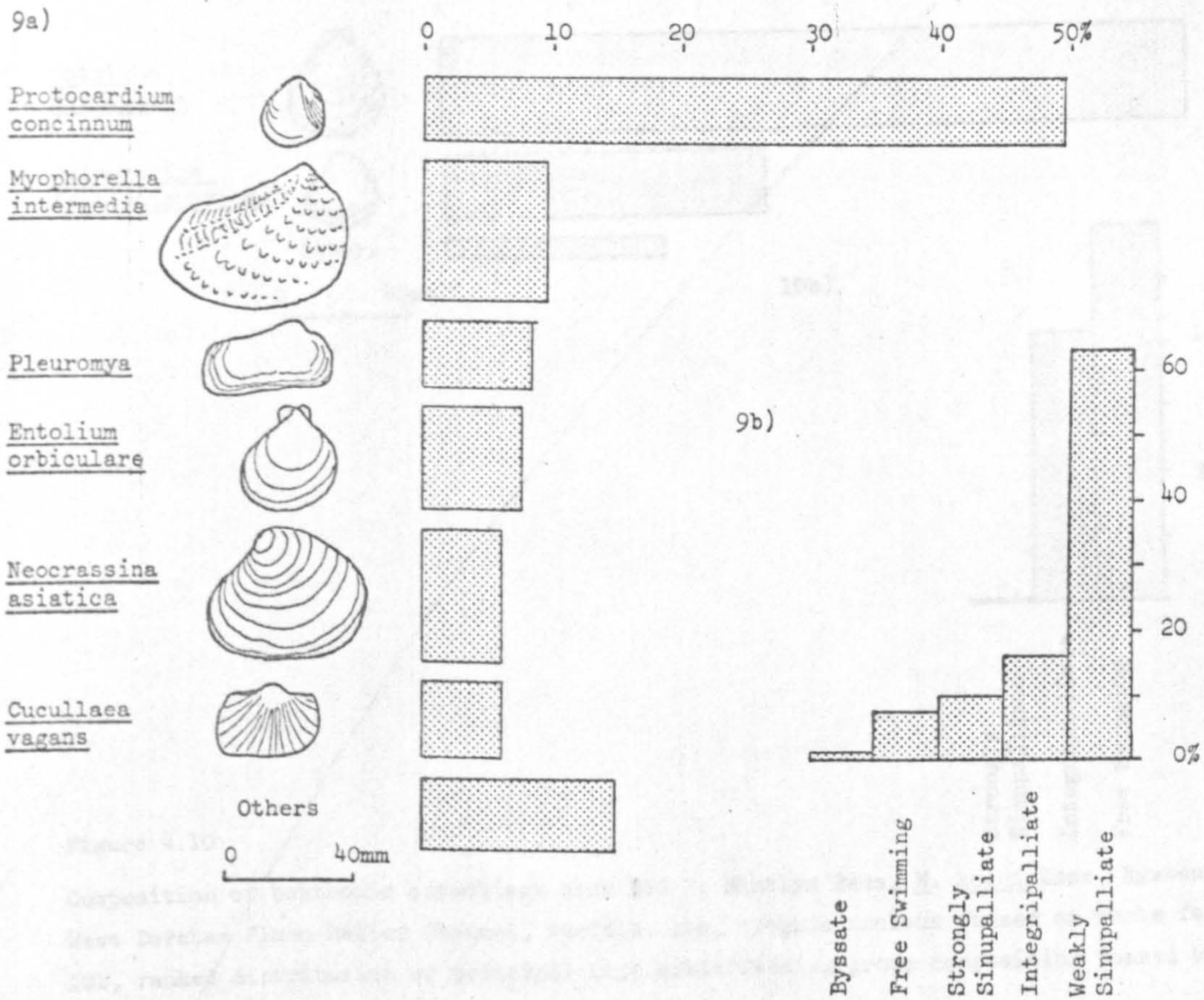


Figure 4.9

Composition of benthonic assemblage from Basal Mintlyn Nodule Bed, Ryazanian, North Runcton, Norfolk. 9a, trophic nucleus (based on whole fauna). 9b, ranked distribution of principal life habit/feeding group composition (based on bivalves only).

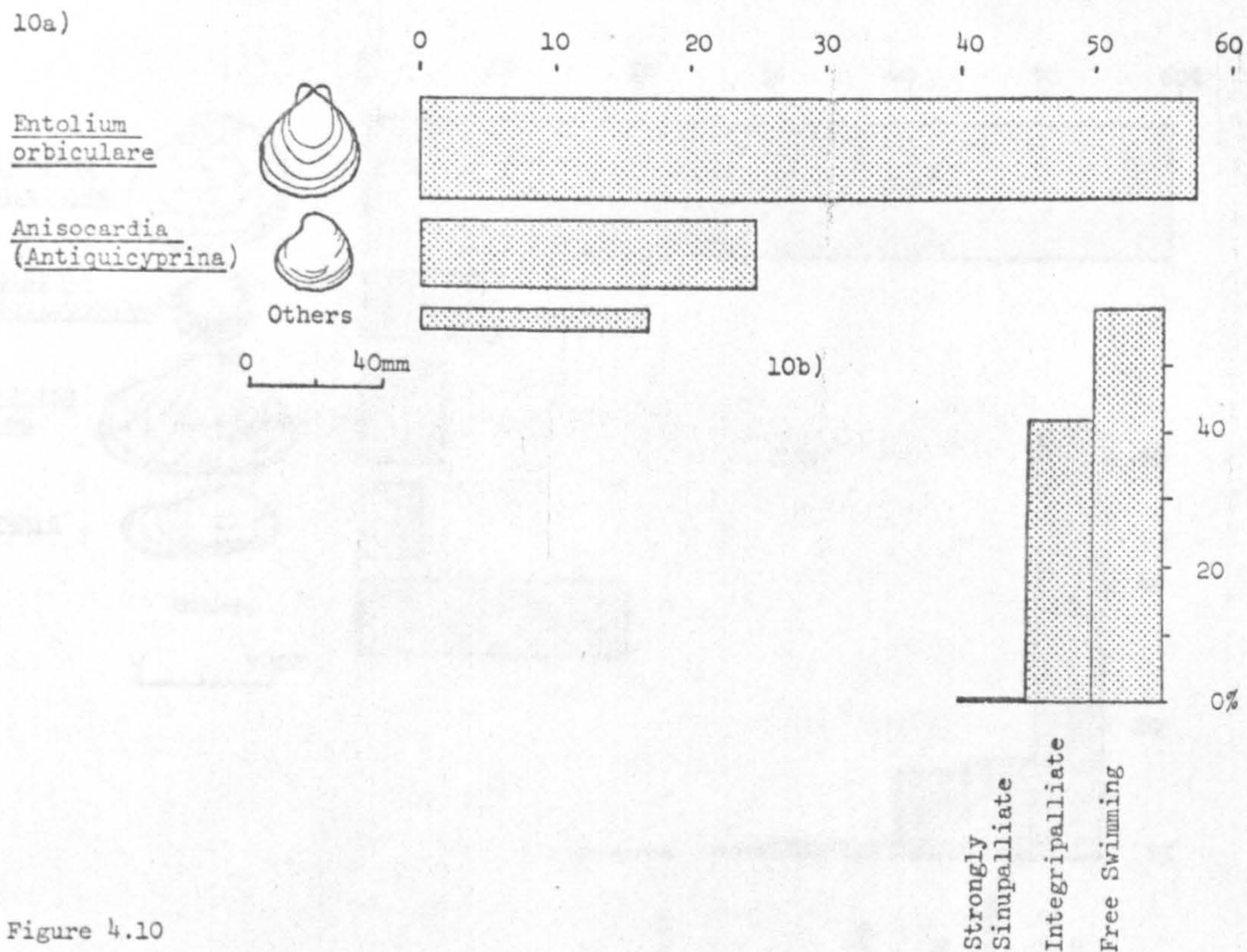


Figure 4.10

Composition of benthonic assemblage from Bed 7, Mintlyn Beds, *H. kochi* Zone, Ryazanian, West Dereham Flood Relief Channel, Norfolk. 10a, trophic nucleus (based on whole fauna). 10b, ranked distribution of principal life habit/feeding group composition (based on bivalves only).

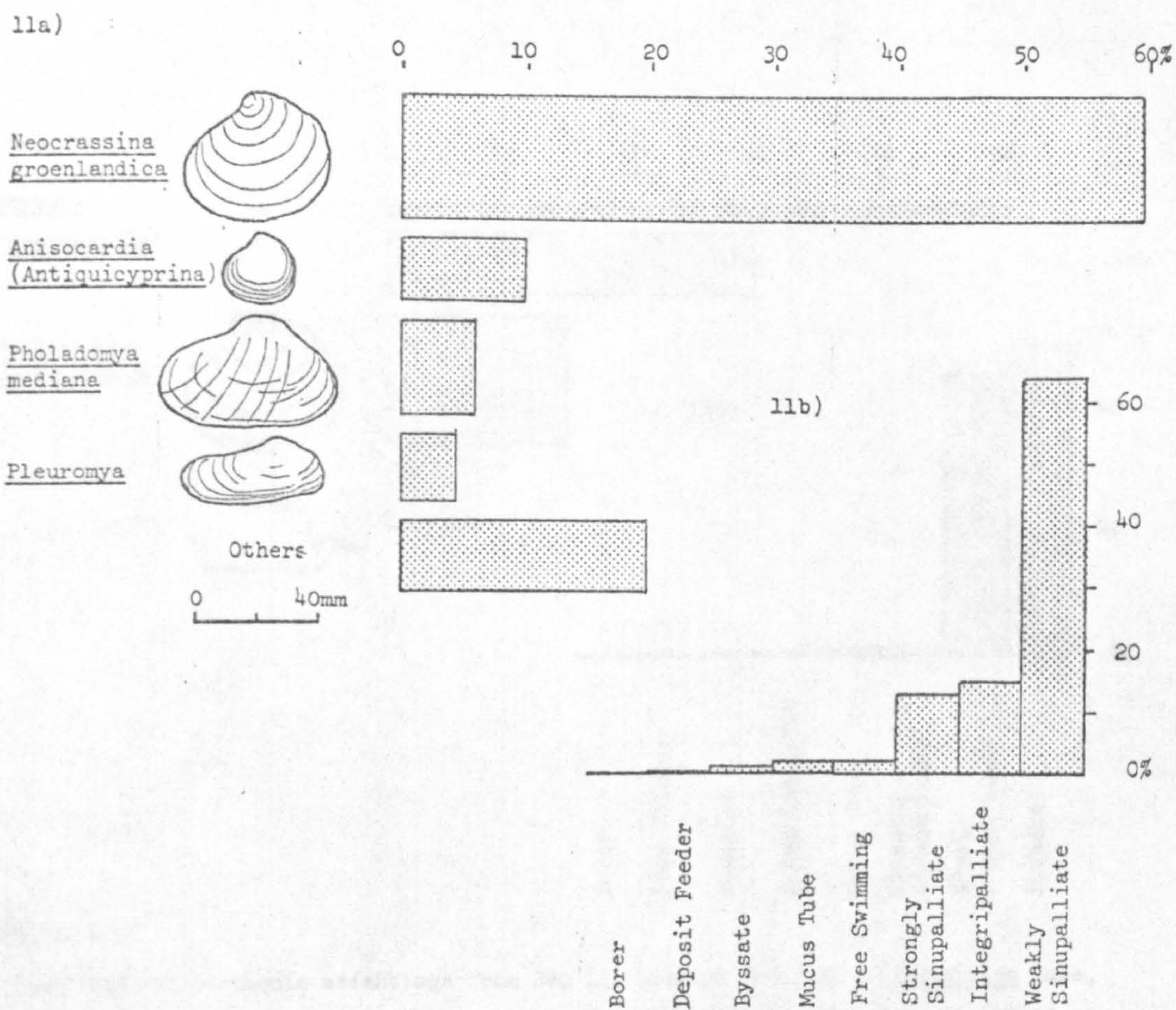


Figure 4.11

Composition of benthonic assemblage from sideritic concretions in the clay-ironstone facies of the Mintlyn Beds, H. kochi Zone, Ryazanian, Flood Relief Channel, West Dereham, Norfolk. 11a, trophic nucleus (based on whole fauna). 11b, ranked distribution of principal life habit/feeding group composition (based on bivalves only).

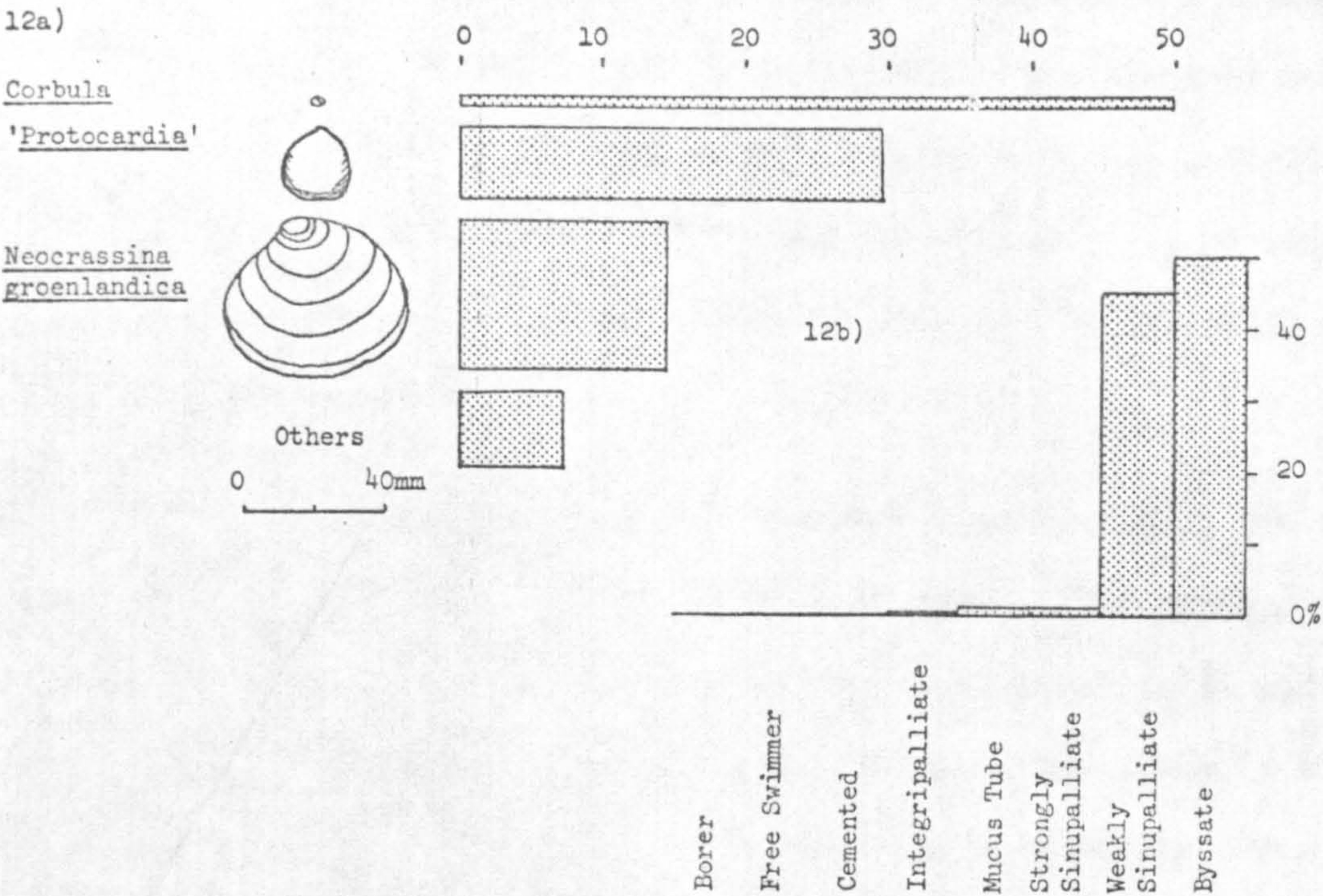


Figure 4.12

Composition of benthonic assemblage from Bed 11, Mintlyn Beds, S. stenomphalus Zone, Ryazanian, King's Lynn Bypass, Mintlyn Wood, Norfolk. 12a, trophic nucleus (based on whole fauna). 12b, ranked distribution of principal life habit/feeding group composition (based on bivalves only).

it is found in the basal Spilsby Nodule bed. The horizon is composed of dark phosphatised nodules up to 120 mm diameter, set in a glauconitic silty sand with some quartzitic and lyditic pebbles. The variety of lithology provides two main ecological niches. The first is based on the hardgrounds provided by the exhumed phosphatised nodules lying on the sediment surface. They provide attachment areas for cemented bivalves and sites suitable for boring forms. The abundant byssate fauna was almost certainly attached largely to these nodules. The second niche is provided by the silty sands in which a rich infauna developed.

Although Pleuromya is the most abundant bivalve (20%), the byssate bivalvia make up the dominant feeding/life habit group. The byssate Grammatodon schourovskii is the second most important taxon (11%) and is therefore used with Pleuromya to name the assemblage. The fauna is the most diverse recognised in the Spilsby basin having a Diversity Index of 13.5,) and a trophic nucleus of 13 taxa. The trophic nucleus contains in addition to the dominant bivalvia, serpulids, gastropods and brachiopods.

Frequently Grammatodon and Hiatella may be found (as phosphatised internal moulds) with paired valves in occlusion in the Basal Spilsby nodule bed. This is unusual for byssate forms. It is believed here that the shells were living attached to phosphatised nodules on the sea floor. A phase of sedimentation overwhelmed the nodules and the sessile epifauna was entombed. Subsequent sediment pause allowed concentration and precipitation of phosphorite within the local reduced zone defined by the shell valves. Dissolution of the calcite shell followed and the internal mould was mixed with earlier phosphatic nodules in a further phase of condensation.

The deep burrowing Pleuromya was presumably still in life position

when the internal mould became phosphatised. Subsequent winnowing and condensation concentrated the individuals in the basal nodule bed. The common mucus tube feeder, Discoloripes, probably lived at a similar depth to Pleuromya and was likewise phosphatised before condensation. Shallow burrowers are relatively well represented within the trophic nucleus (Anisocardia, Pressastarte and Hartwellia). The valves are normally found dissarticulated presumably principally by bioturbation in the near surface zone of the sediment. It is unlikely that current sorting has selectively removed elements of this part of the assemblage as the byssate epifauna would have suffered to a much greater extent. The paucity of free swimmers such as Entolium is believed to be primary as the area where one would expect Entolium to be the most likely candidate for current removal i.e. sands, is the facies in which the genus abounds. Although it is possible that Gastrochaena could be the principal rock boring organism in the basal nodule bed the byssate Hiatella seems to be the main occupant of the borings. (See description of Hiatella in chapter 3).

Although this assemblage has only been examined in detail in Nettleton, museum collections indicate the presence of elements of the assemblage in Bedfordshire (reworked into the basal Aptian deposits), in the base of the Sandringham Sands south of the Wash where it appears to be highly reworked, in Lincolnshire and in the Coprolite bed at the base of the Speeton Clay.

3b.ii. Entolium assemblage (Figs. 4, 4a, b; 4.5a, b; 4.6a, b; 4.10a, b)

Entolium dominated assemblages occur in the medium to coarse grained glauconitic and lithologies in the Spilsby basin. Four horizons

have been studied in detail, namely the P. oppressus Zone erratic calcareous concretions of Leziate, the S. preplicomphalus Zone calcareous concretions of West Keal, the S. lamplughi Zone calcareous concretions of Nettleton and the fine sand concretions from immediately above the base of the H. kochi Zone, West Dereham.

In the medium to coarse grained sands of West Keal and Nettleton, Entolium is overwhelmingly dominant (51-57%). The rest of the taxa each represent less than 9%. Whole Entolium pavements may be found with current oriented valves all convex upwards. Entolium would have been able to maintain its position on the sediment surface by short swimming movements to keep pace with sedimentation. The relatively mobile substrate would tend to discourage normal shallow burrowers. Deeply burrowing elements such as Pleuromya and Pholadomya are relatively common in life position, and although the near-surface sediment must have been continually reworked by currents, the depth of burial of these burrowers must have kept them from exhumation. The semi-infaunal Pinna is also occasionally found in life position. One such specimen was found containing several gastropods. Sowerbya with its thick shell, closed margins and deep pallial sinus must have been an active burrower within the reworked top zone of the sediment. It is rarely found with valves in occlusion and on death is normally disarticulated.

The faunal diversity of the West Keal and Nettleton concretions is relatively high, being 9.4 and 7.3 respectively with relatively high numbers of taxa within the trophic nuclei, 12 and 7 respectively.

In the Leziate concretions, the Entolium proportion is less developed (28%). The sediment is a medium-grained sand with a relatively high proportion of phosphatised pebbles reworked into the base from the

Basal Spilsby Nodule Bed below. Although integripalliate bivalves are the second most abundant bivalve group represented, (20%), the large pedunculate brachiopod Rouillieria is the second most abundant of the trophic nucleus. The coarser nature of some of the substrate at Leziate than at Nettleton and West Keal accounts for the higher proportion of the cemented and byssate bivalve fauna and presumably indicates a slightly more stable bottom. Some of these forms may also have used living or dead bivalve shells for attachment (e.g. Pinna). The diversity of this unit is high (11.2) and so is the number in the trophic nucleus (9). The graph of the feeding groups (Fig. 4.6b) like that of the basal Spilsby nodule bed indicates one of the more even distributions between the principal feeding types represented in the Spilsby fauna.

These first three examples of the Entolium assemblage in medium- to coarse-grained sands suggest a very shallow environment within the active zone of wave base activity. The paucity of lignite and of fine sediment suggest some type of shallow offshore winnowed sand bar complex. The presence of such trace fossils as Ophiomorpha in these sands could be used to indicate even low intertidal conditions as Kennedy and Sellwood (1971) postulate for the Reading Beds.

The fourth Entolium dominated assemblage (Fig. 4.10a, b) is sampled from a sand concretion horizon low in the H. kochi Zone before the development of the clay-ironstone facies later within the same zone. It is a medium to fine grained sand which is crowded with relatively small Entolium, (57%) occasional Anisocardia and local patches of disarticulated Nicaniella. A small proportion of lignite indicates proximity of source region. This appears to be a depleted fauna as the faunal diversity only 2.3 and there

are only two species in the trophic nucleus. This may represent a near shore sand bar which is winnowed and current-sorted, although the thinness of the bed may indicate a more sheet-like sand feature.

Although Entolium-dominated assemblages have only been well studied at four sites, it is believed that the assemblage is widespread within the pure sand facies especially of the Spilsby Sandstone. Visually estimated Entolium dominated sands are also recorded from S. preplicomphalus Zone concretions from Leziate (derived) and Harrington Hall, and from the topmost Lower Spilsby Sandstone of Donnington.

3b.iii. Lyapinella assemblage (Figs. 4.7a, b; 4.11a, b)

The Lyapinella dominated assemblage is named after the principal bivalve Neocrassina (Lyapinella). Lyapinella is used instead of Neocrassina to name the assemblage to avoid confusion with other subgenera of Neocrassina. The assemblage is recognised in two horizons of contrasting facies. The first is in the condensed Subcraspedites horizon, S. lamplughi Zone of West Dereham. The second is in the clay ironstone facies of the Mintlyn Beds, H. kochi Zone, of the same locality.

The Subcraspedites horizon is composed of a conglomerate of blackened phosphatised internal moulds of bivalves, ammonites and reptile bones, with some large fragments of bored lignite. The phosphatised moulds are preserved in a medium-grained sand cemented by phosphorite. The matrix to the phosphatised material is a medium-grained silty glauconitic sand. Lyapinella overwhelmingly dominates the assemblage (45%); other shallow burrowing genera (Dicranodonta, Anisocardia and Hartwellia) together with deep burrowing Pleuromya comprise the trophic nucleus. Mucus tube feeders,

byssate, shell and wood boring and free swimming forms make up less than 3% each of the whole fauna. The whole fauna has a Diversity Index of 6.6. The sediment is a clayey glauconitic sand. The fine fraction would have discouraged the spat of byssal bivalves, although there must have been a certain amount of dead shell material on the sea floor projecting through the sediment to allow Gastrochaena to make borings. The clay present would also discourage the presence of Entolium. It therefore appears that the nature of the substrate encouraged a burrowing bivalve fauna. The dominance of shallow burrowing suggests that this fauna is largely intact having been phosphatised in situ after being overwhelmed by a phase of sedimentation and then winnowed out and concentrated without large scale transport as the moulds are relatively fresh. There does not appear to have been time for the moulds to have been bored or infested by cemented bivalves before further sedimentation caused their final burial. The drifted lignite may have been transported a considerable distance to allow the attack of Martesia. The driftwood fragments are also considerably waterworn, in contrast to the bivalves, and therefore do not necessarily indicate the proximity of land. The sediment and fauna suggest a shallow shelf facies.

In the clay ironstone concretions of the upper part of the H. kochi Zone at West Dereham, the bivalve fauna is preserved as decalcified moulds. The matrix is a purple to green fine sandy glauconitic sideritic clay ironstone, and commonly contains fine disseminated lignite. Phosphatisation occurs in local patches but does not appear to have been exposed on the sea bed and remains a pinky-brown colour. Lyapinella represents 59.5% of the fauna. The trophic nucleus contains in addition only Anisocardia, Pholadomya and Pleuromya. As in the Subcraspedites horizon the infauna dominates the assemblage, while free swimming, byssate and mud borers are present in very

reduced numbers. It is interesting to note that this is the only studied horizon in which nuculid bivalves have been found. However these deposit feeders compose only 0.58% of the whole benthonic fauna. The assemblage has a Diversity Index 7.8, but a relatively low trophic nucleus of 4. Deposition probably took place under moderately quiet marine conditions, although perhaps in some type of lagoonal environment to allow iron enrichment of the sediment perhaps by iron fixing bacterial action. The primary source of iron may be from rivers draining the London Midlands area.

The two studied examples of N. (Lyapinella) assemblages show that the bivalve dominates in clayey sediment in which sand may be absent or present. Contemporary sediments to the north are much uniformly coarser sands and may have been acting as a barrier to the more sheltered area of Norfolk.

3b.iv. Protocardia dominated assemblage (Figs. 4.8a, b; 4.9a, b)

Protocardia overwhelmingly dominates the basal Cretaceous nodule bed in Norfolk. The assemblage has been sampled at West Winch and North Runcton and although the trophic nucleus components vary slightly from one location to the other, the bivalve feeding groups plot as almost identical distributions. The benthonic faunas have diversity indices of 6.9 and 5.8 respectively, while the trophic nuclei are 4 and 6. Individual species each occupy less than 10% of the benthonic fauna. The trophic nuclei contain a combination of shallow burrowers (N. (Lyapinella), Corbicellopsis, Myophorella and C. (Dicranodonta)), a deeper burrower (Pleuromya), and the free swimming Entolium. The sediment suggests a soft bottom predominantly sandy with glauconite and a subordinate amount of clay which has become phosphatised.

The sediment appears to be more sandy than that described under the Lyapinella assemblage. As a consequence the free-swimming group appears within the trophic nucleus at North Runcton, but byssate forms are still not well represented in the relatively mobile substrate. The degree of phosphatisation is believed to be partially due to the variation in clay component of the sediment. There does not appear to be any significant reworking of the fauna and there is not the blackening that has taken place in the Subcraspedites band. Even the remains of the shallow burrowing Protocardia are almost always complete with valves occluding. However it is possible that some of the byssate epifauna may have been removed selectively by currents.

The Protocardia assemblage appears to be transitional between the Lyapinella assemblage of the Subcraspedites horizon and the Entolium assemblage typical of the sands of the Spilsby Sandstone. The lithology and fauna indicate a shallow marine environment with a slightly clayey sand relatively free from terrigenous lignite.

3b.v. Corbula dominated assemblage (Fig. 4.12a, b)

Corbula has only been found dominating the benthonic assemblage in the S. stenomphalus Zone of the Mintlyn Beds, Mintlyn Wood, Kings Lynn bypass cutting. The genus is normally a scarce representative of the Spilsby fauna. The lithology is a silty clay ironstone, purple when fresh, weathering yellow-brown and which superficially resembles the clay ironstone facies of the H. kochi Zone described under the Lyapinella assemblage. Large fragments of lignite are commonly up to 150 mm long and there is also much fine comminuted material. The trophic nucleus is composed of Corbula (50%), 'Protocardia' (30%) and N. (Lyapinella) (15%). The rest of the species each

occupy less than 1.5% of the benthonic fauna. Deep burrowing forms are represented by Thracia and Pleuromya. The bottom appears to be soft and one fresh complete specimen of Pinna was seen which could have been a typical attachment site for the sparse byssate fauna. Some ostreids were seen infesting a Camptonectes (Boreionectes) shell. Apart from the peculiar byssate shallow burrowing Corbula this fauna is generally similar to that from the H. kochi Zone clay ironstone facies, but is more restricted in diversity (5.5) and with only three species in the trophic nucleus. This indicates a very near shore quiet marine lagoonal facies which is more restricted than that of the kochi Zone.

4. Discussion of the assemblages.

4a. Trophic Nucleus (whole benthos)

The trophic nucleus (Neyman 1967) is defined as the numerically dominant taxon which make up 80% of the fauna. It provides a figure of the relative proportions of the characteristic taxa of each assemblage. Strictly it should be examined from the point of view of biomass, however this is difficult for the palaeontologist to calculate. Therefore the numerical abundance is used for the order but it is modified by showing the results as a relative size (of the taxa) histogram as used by Duff (1975). The results are shown in figures 4.3a and 4.12a. The number of species comprising the trophic nucleus also gives a value comparable to the Diversity Index discussed below (see Figure 4.2).

4b. Trophic group composition (bivalves only)

The bivalvia belong to relatively limited trophic groups. On the simplest level they can be divided between deposit feeders and suspension

feeders. If the suspension feeders are subdivided into epifaunal and infaunal elements, triangular plots can be divided between deposit feeders, infaunal and epifaunal suspension feeders (fig. 4.13a, b). It can be seen that deposit feeders are not a significant feature of the strata under consideration, and the plots are effectively divided between the infaunal and the epifaunal suspension feeders. Figure 4.13a shows the assemblages from impure sands and clays plotting close to the 100% infauna. The Basal Spilsby Sandstone plots at 44% epifauna, while the pure sands plot between 56 and 73% epifauna. By removing the Free swimming suspension feeders (principally Entolium) and replotting Fig. 4.13b, the results show a very close correlation between the average grain size and the proportion of epifauna. Clearly the finer-grained the deposit, the more likely infauna is to dominate. The increasing size of local hard substrates gives increasing opportunity for attachment of epifauna regardless of intervening muddy patches.

On a more detailed level, the trophic groups of the bivalves can be further subdivided to give a closer relationship between the life habit/feeding groups and the substrate (Kauffman in Moore Ed. 1969). The trophic group plots for the bivalves are shown in figures 4.3b - 12b. Examination of the trophic groups of different assemblages will emphasize similarities in feeding type that are masked by the slightly different generic and specific compositions. For example compare the trophic groups of the two examples of the Protocardia dominated assemblage and the two examples of the Lyapinella dominated assemblage which show that both major assemblages are very similar from the trophic group point of view although there are individual differences which are picked out by particular species.

a. All Bivalves

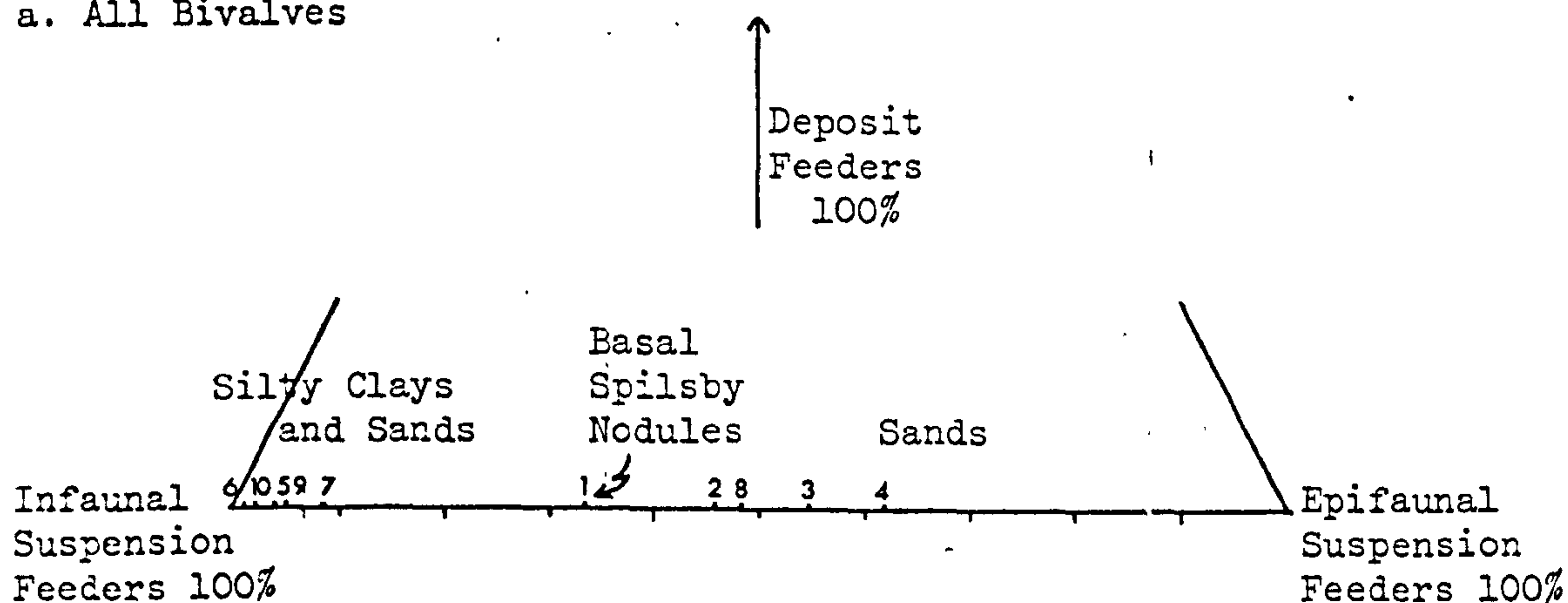
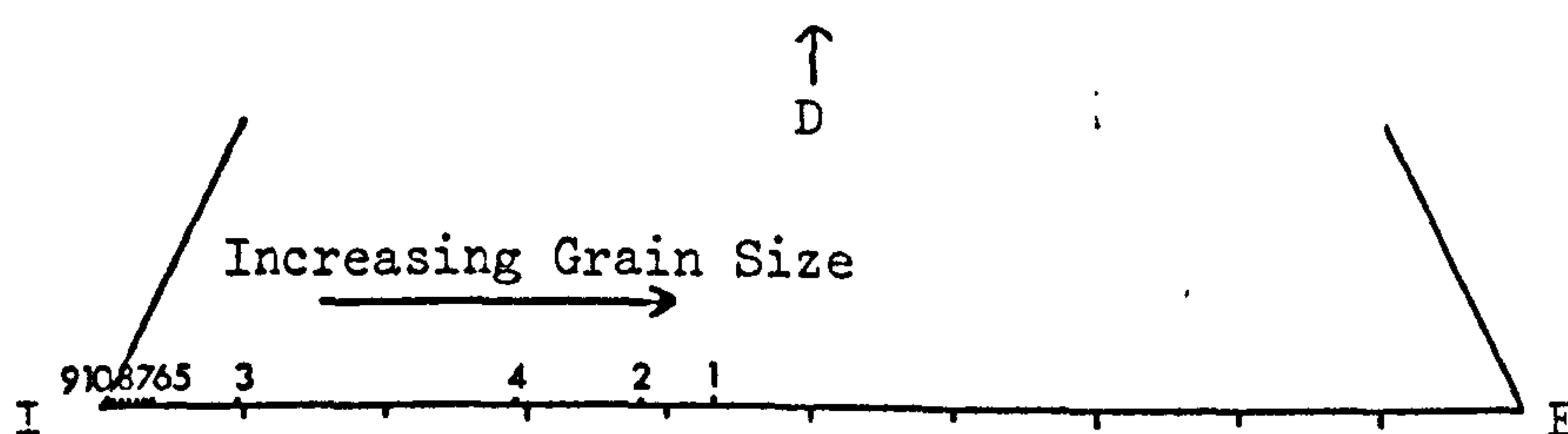
b. All Bivalves, excluding Free Swimmers (Entolium)

Figure 4.13

Triangular plots of bivalve feeding groups, showing distribution of 10 analysed assemblages between deposit feeders, epifaunal suspension feeders and infaunal suspension feeders. Figure a shows distribution for whole bivalve assemblages and b shows the same assemblages with the free swimmers (Entolium) removed.

By ranking the trophic group abundances of different assemblages, one is able to construct a picture of the preferred environment of a trophic group. These ranked distributions are shown in figures 4.15 - 20, and are discussed briefly below.

4b.i. Free Swimming Epifaunal Suspension Feeders. Figure 4.14

Free swimming bivalves of the Spilsby environments show a marked preference for clean sandy bottom conditions where they generally dominate the benthonic assemblage. The presence of clay discourages them perhaps because of its adhesive properties, or because a turbid environment clogs their filtering mechanism.

4b.ii. Byssate Suspension Feeders. Figure 4.15

Byssate bivalves prefer coarse gravelly substrates and decrease in abundance with grain size being suppressed by the presence of a clay fraction which presumably causes turbid bottom conditions. The exceptional high proportion of byssate suspension feeders in the stenomphalus Zone of Mintlyn wood is due to the presence of the peculiar byssate shallow-burrowing infaunal Corbula.

4b.iii. Cemented Epifaunal Suspension Feeders. Figure 4.16

Because of the relatively unstable bottom conditions within the Spilsby basin, cemented bivalves are not well represented. Their appearance is largely fortuitous when a local hardground in the form of an exhumed phosphatised nodule or dead shell has remained exposed for sufficient time to allow infestation and development of the individual. Turbidity preference within the group is probably variable. The small Liostrea probably tolerated

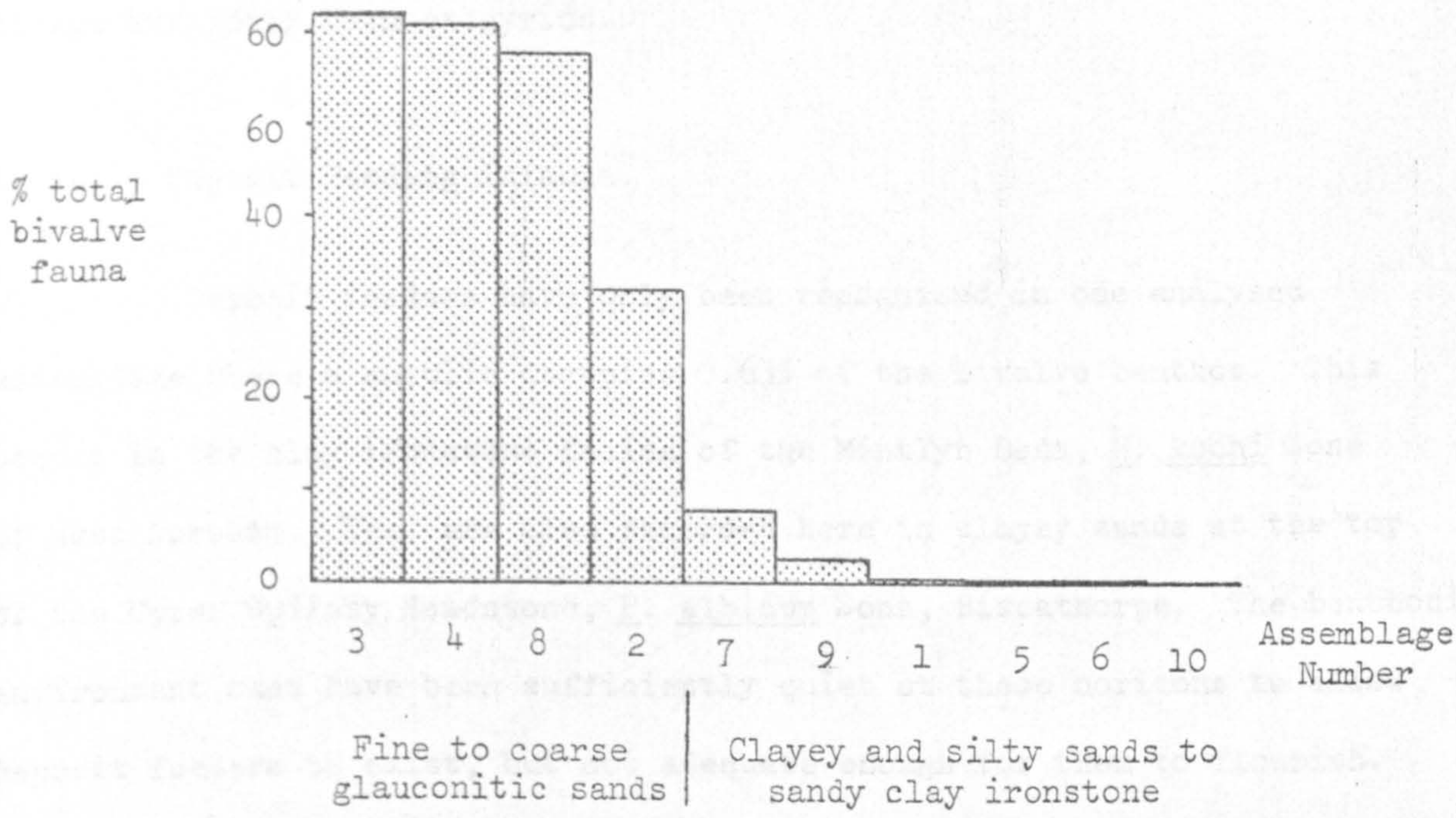


Figure 4.14

Ranked histogram of Free Swimming proportion of bivalves in assemblages listed in Figure 4.2.

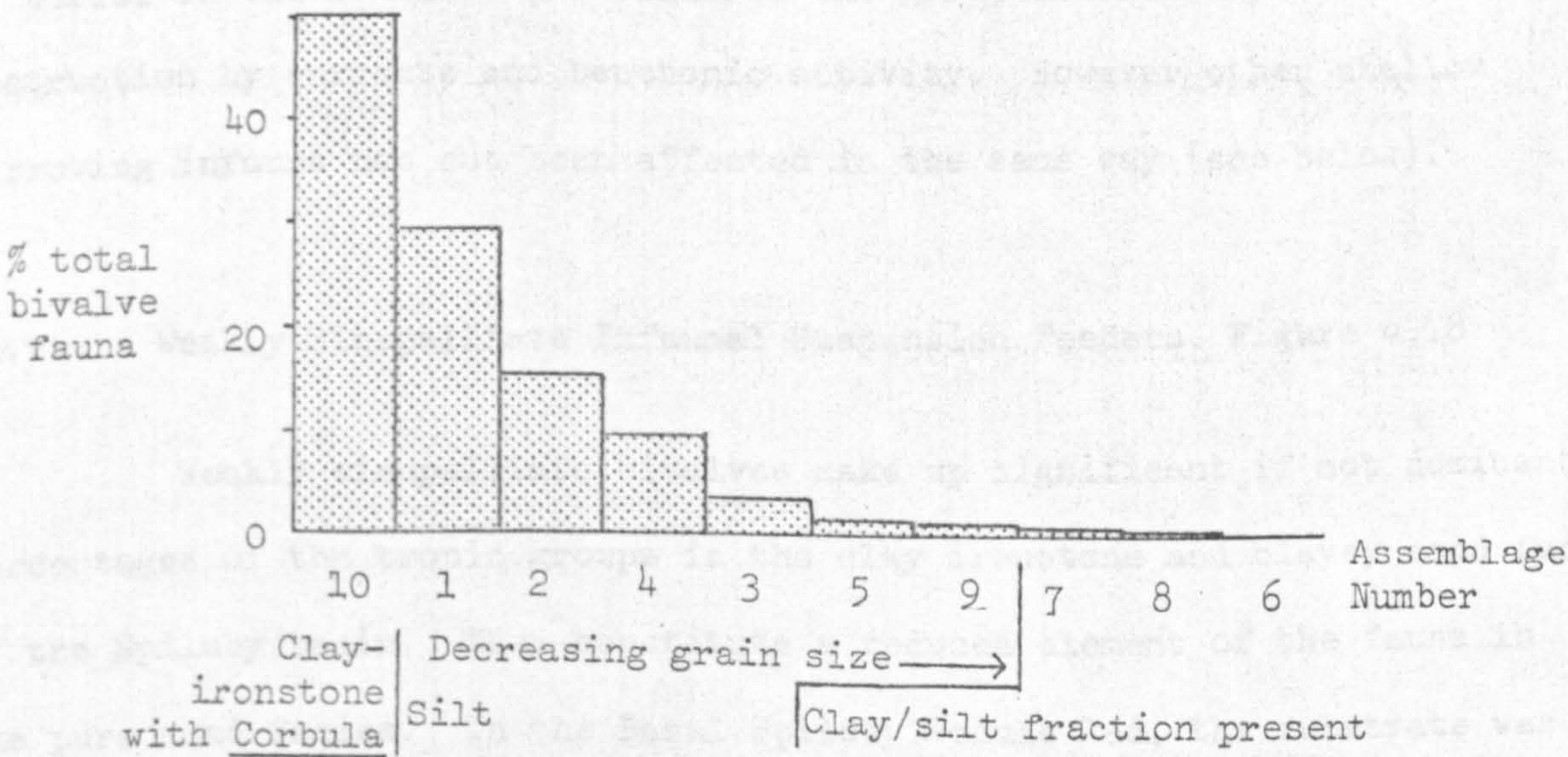


Figure 4.15

Ranked histogram of Byssate proportion of bivalves in assemblages listed in Figure 4.2.

higher turbidity than exogyrids.

4b.iv. Deposit Feeding Infauna.

Deposit feeders have only been recognised in one analysed assemblage where a nuculid occupies 0.63% of the bivalve benthos. This occurs in the clay ironstone facies of the Mintlyn Beds, H. kochi Zone of West Dereham. They are also recorded here in clayey sands at the top of the Upper Spilsby Sandstone, P. albidum Zone, Biscathorpe. The benthonic environment must have been sufficiently quiet at these horizons to allow deposit feeders to exist, but not adequate enough for them to flourish.

4b.v. Integripalliate Infaunal Suspension Feeders. Figure 4.17

Integripalliate forms do not appear to follow any distinct patterns of distribution. They are moderately successful in most environments studied, but never dominate them. There is a possibility that the shallow position of burial in the sediment has rendered the group liable to postmortal destruction by currents and benthonic activity. However other shallow burrowing infauna has not been affected in the same way (see below).

4b.vi. Weakly Sinupalliate Infaunal Suspension Feeders. Figure 4.18

Weakly sinupalliate bivalves make up significant if not dominant percentages of the trophic groups in the clay ironstone and clayey sand facies of the Spilsby basin. They constitute a reduced element of the fauna in the pure sand facies. In the Basal Spilsby Nodule Bed, the substrate was probably too consolidated for this group to thrive, and the presence of phosphatised nodules may have hindered burrowing.

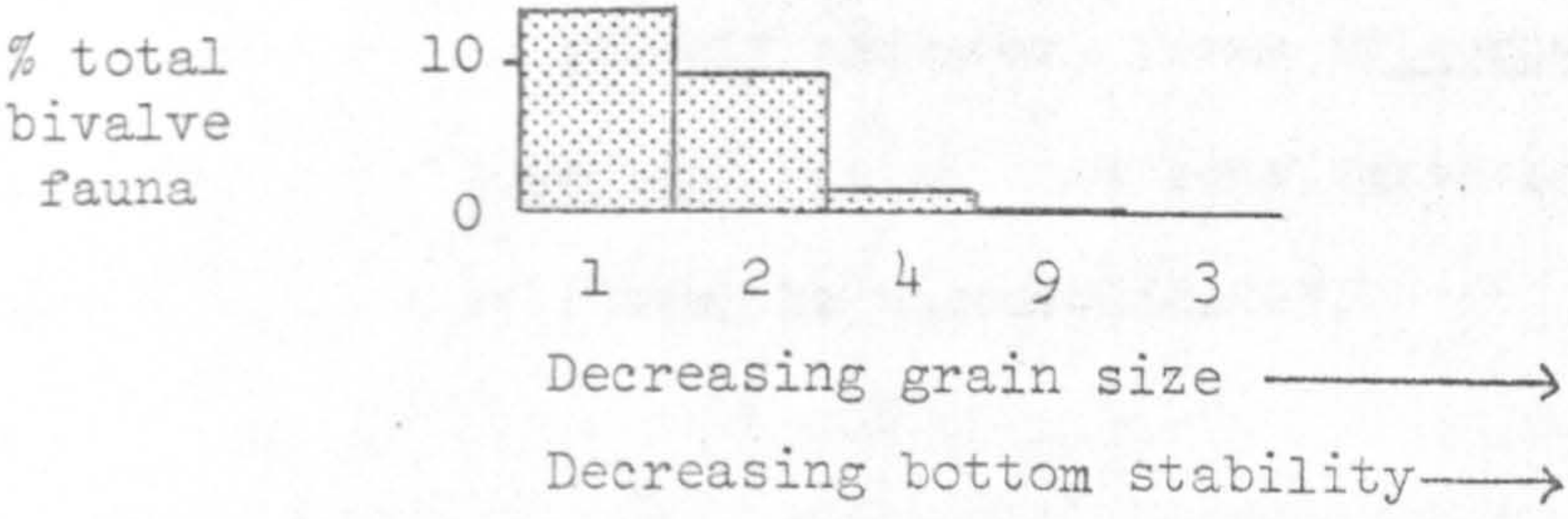


Figure 4.16

Ranked histogram of cemented proportion of bivalves in assemblages listed in Figure 4.2.

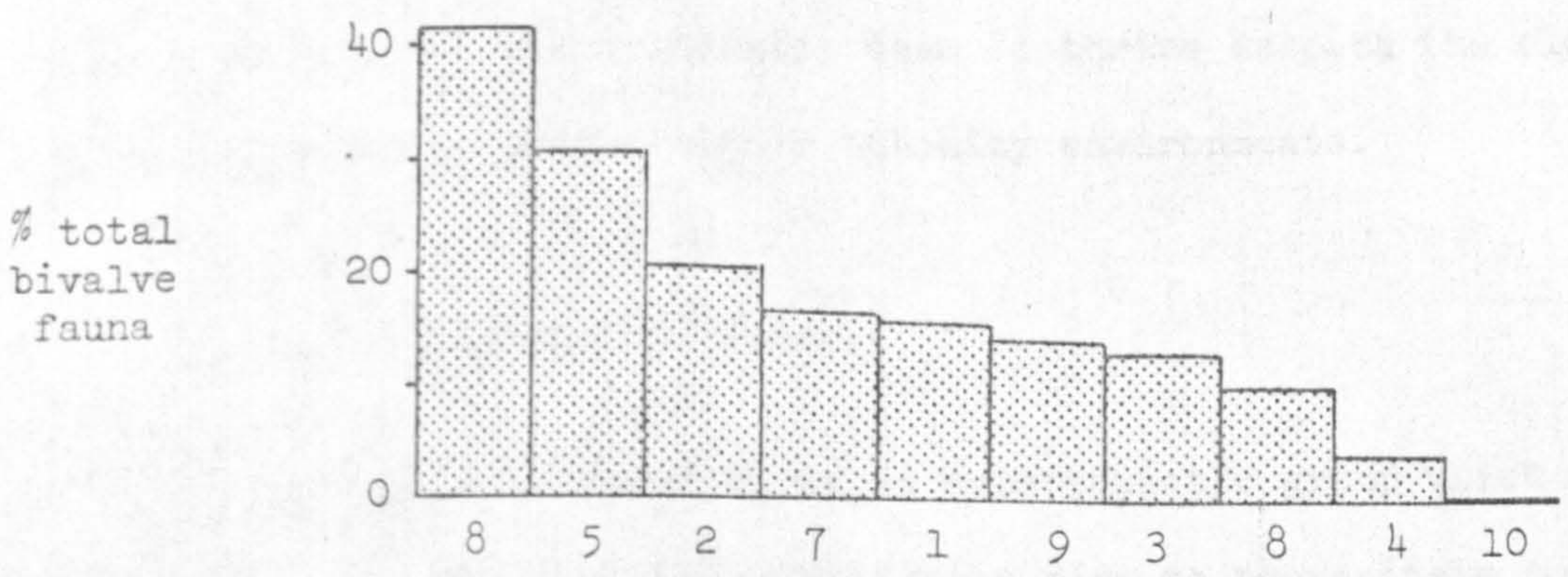


Figure 4.17

Ranked histogram of integripalliate proportion of bivalves in assemblages listed in Figure 4.2.

4b.vii. Strongly Sinupalliate Infaunal Suspension Feeders. Figure 4.19

Although only a dominant faunal element in the basal Spilsby Nodule Bed, strongly sinupalliate forms make up a low profile histogram indicating a broad preference for low turbidity environments. The group includes both relatively sedentary forms (Pleuromya and Pholadomya) and active forms (Sowerbya) which show some variation in substrate type from moderately consolidated to unconsolidated.

4b.viii. Mucus Tube Suspension Feeders. Figure 4.20

The mucus tube feeders belong to two principal groups. Firstly the lucinids occupy a small proportion of the generally pure sand facies. Secondly the thraciids occupy a similiar small proportion of the fauna in the clay ironstone facies of Norfolk. Both groups are found in the basal Spilsby Nodule Bed where lucinids seem to thrive despite the clay content. Thracia appears to prefer higher tubidity environments.

4b.ix. Boring Suspension Feeders.

The borers appear to be an opportunistic group which can only thrive when the sediment is sufficiently firm to necessitate boring as opposed to burrowing, or when hard grounds such as dead thick shells or phosphatised nodules are exhumed and remain exposed for sufficient time to allow infestation and inhabitation. Drift wood can be attacked either when still floating or when waterlogged and resting on the sea floor. Traces of boring bivalves are locally abundant where the conditions allowed survival, but only rarely are the borings found inhabited and only in the basal Spilsby nodule bed are they commonly infested, but even then it is believed to be

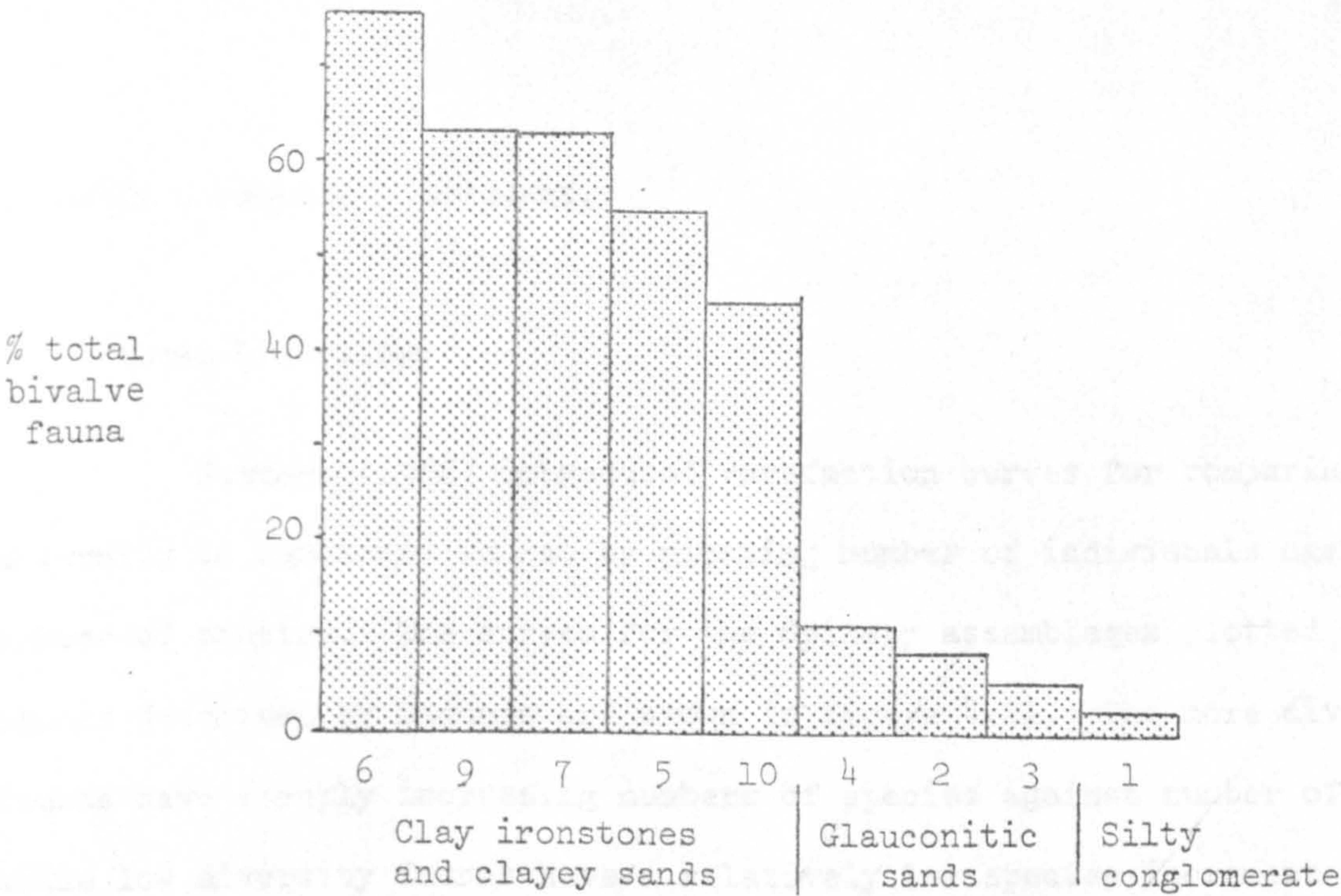


Figure 4.18
Ranked histogram of Weakly Sinupalliate proportion of bivalves in assemblages listed in Figure 4.2.

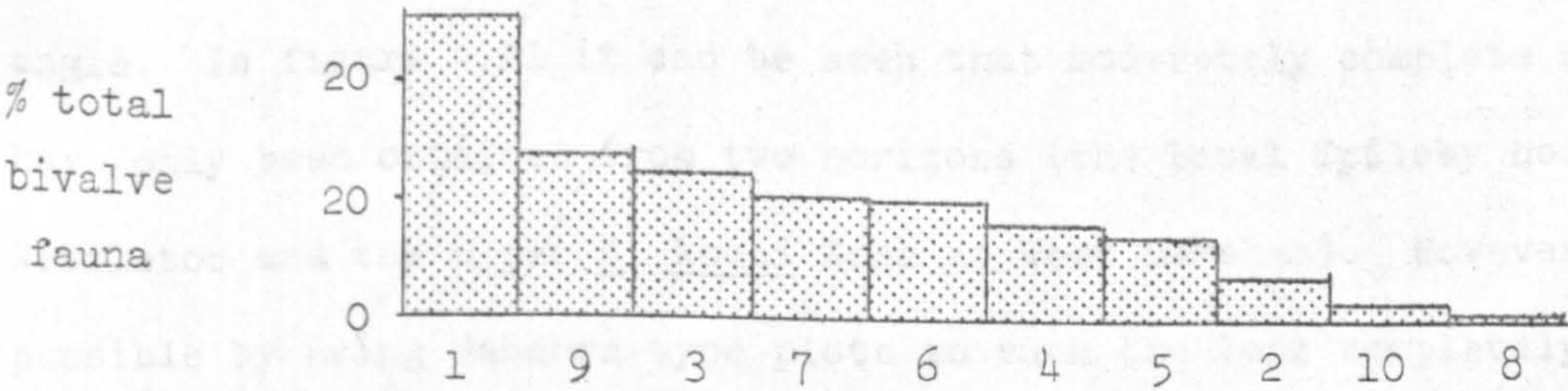


Figure 4.19
Ranked histogram of Strongly Sinupalliate proportion of bivalves in assemblages listed in Figure 4.2.

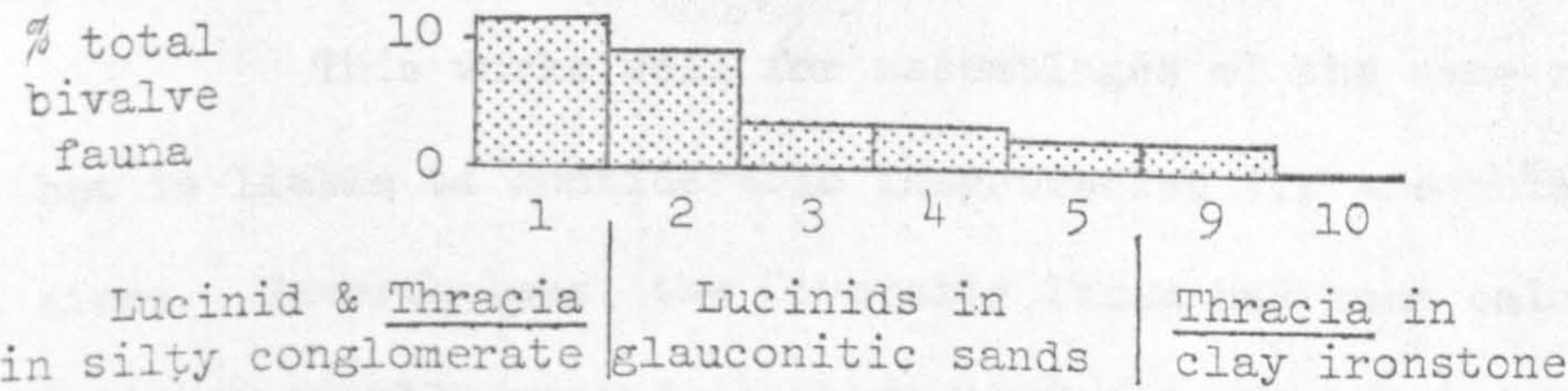


Figure 4.20
Ranked histogram of Mucus Tube Feeders proportion of bivalves in assemblages listed in Figure 4.2.

normally a secondary occupant.

5. Faunal Diversity.

Sanders (1968) introduced rarefaction curves for comparing faunal diversity in benthonic faunas by plotting number of individuals against number of species. The curves for the Spilsby assemblages plotted in the manner described by Sanders are shown in figure 4.21. The more diverse faunas have steeply increasing numbers of species against number of individuals, while low diversity faunas have a relatively low species increment versus number of individuals. The technique also gives a visual impression of the completeness of the collected assemblage. In a complete assemblage the graph levels out as the maximum number of species is approached. If the maximum of species is not approached, the graph still rises at a relatively high angle. In figure 4.21 it can be seen that moderately complete assemblages have only been obtained from two horizons (the basal Spilsby nodule bed at Nettleton and the upper H. kochi Zone at West Dereham). However it is possible by using Sanders type plots to rank the less completely collected assemblages of the other horizons by the slope of their respective graphs. Their order of rank of diversity is given in Figure 4.2.

Diversity Index has been defined by Ziegler et al. (1968) as:

$$\frac{\text{no species}}{\log. \text{ no. individuals}}$$

This works well for assemblages of the same size as each other, but is liable to considerable inaccuracies for assemblages of different sizes. Nevertheless, the Diversity Index has been calculated for the Spilsby assemblages and is shown ranked in Figure 4.2. The order obtained

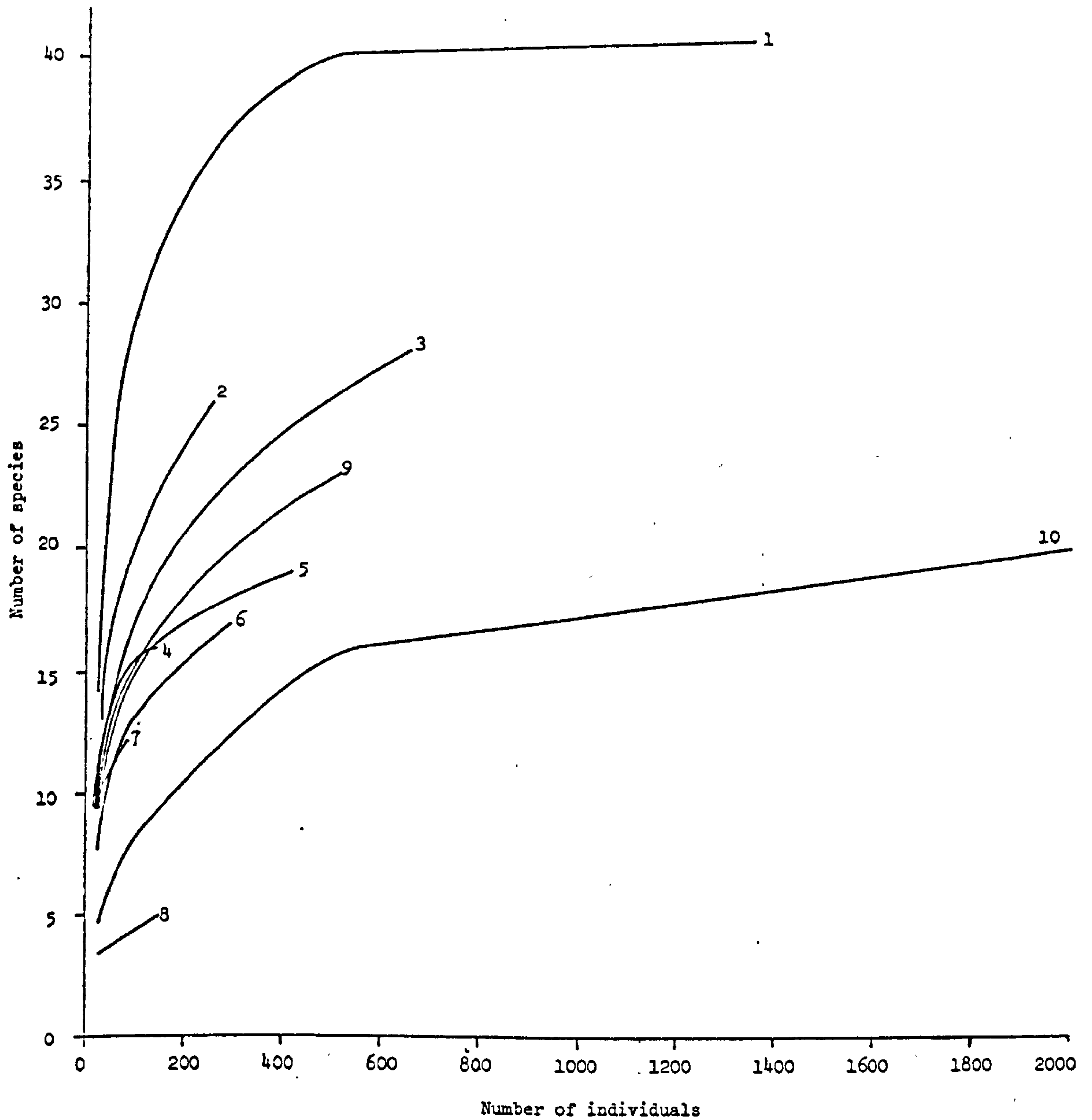


Figure 4.21

Graph of number of species plotted against number of individuals for the numbered assemblages listed in figure 4.2, showing general decrease in diversity from Middle Volgian to Ryazanian times in eastern England. Lines plotted according to the technique of Sanders (1968).

by ranking is identical to that obtained by ranking rarefaction curves except for one pair of values. It is therefore moderately accurate despite the variation in size of the assemblages here, and is therefore used in the discussions.

From the few horizons studied, there appears to be a generally decreasing diversity of the fauna from the Basal Spilsby Nodule Bed upwards to the lower part of the H. kochi Zone, which is followed by a weak increase later in the Ryazanian. All the assemblages appear to be fully marine, with distinctive cephalopod faunas. The initial high diversity of the Basal Spilsby Nodule Bed reflects in part the varied benthonic substrate available to the fauna and in part the change from relatively quiet water clays and shales of the Kimmeridge Clay, to the moderately high energy silty sands and nodules of this horizon. It is possible that the fauna represents the accumulated fauna from several original horizons that have subsequently been winnowed and condensed. Although Pleuromya dominates the assemblage, Grammatodon is almost as well represented. The whole fauna is neither overwhelmingly dominated by one species nor even by one trophic group, which would indicate exploitation of the newly formed varied environment by a very wide number of species with varied life habitats. The succeeding P. oppressus Zone concretions are also just dominated by one genus, Entolium, but the fauna is already becoming less diverse. As one goes up through the sands of the preplicomphalus and lamplughi Zones the fauna decreases in diversity and starts to become overwhelmingly dominated by Entolium orbiculare. As the sands become more clayey Entolium is replaced by Protocardia in slightly clayey sands and as the clay continues to increase, Neocrassina (Lyapinella) takes over. As the Spilsby basin matured it appears that certain successful bivalve taxa have been able to dominate at

the expense of other less well adapted taxa.

In the latter part of the H. kochi Zone, when the clay ironstone facies of the Mintlyn Beds appeared, this relatively new environment was exploited by a large number of species and this in turn becomes less diverse with time (Diversity Index 7.8) in the upper part of the H. kochi Zone, and 5.5 in the S. stenomphalus Zone). Both these latter assemblages are overwhelmingly dominated by particular shallow burrowing suspension feeders in both species and trophic groups.

A third indicator of faunal diversity is shown by the overall decrease in number of the taxa in the trophic nucleus from 13 at the base of the Spilsby Sandstone, to 3 in the upper part of the Mintlyn member. The decrease is closely comparable to that already discussed with regard to the Diversity Index and the rank of rarefaction curves.

In comparison to Duff's (1975) plots of rarefaction curves for the benthonic fauna of the Lower Oxford Clay, only the S. stenomphalus Zone assemblage of West Dereham compared closely in Diversity. The other Spilsby assemblages are generally much more diverse which would be expected in a shallower water, higher energy, sandier environment of only slightly different age. Other assemblages in the Jurassic and Cretaceous have yet to be examined from this point of view. However if the results of Rhoads et al. (1972) are taken and partial rarefaction curves are calculated, the curves plot in between the S. stenomphalus Zone plot and those of the Basal Cretaceous nodule bed at West Winch and North Runcton. This is to be expected as Rhoads et al.'s results were taken from Maastrichtian faunas of the central U.S.A. which are interpreted as clayey silt and sand to fine

sands representing delta and bar influenced shelf to offshore bar complex.

Hallam (1976) has plotted generic and specific bivalve abundances through the Jurassic as an index of diversity in western Europe. His results can be modified slightly for his "Tithonian" stage, as shown in fig. 4.22. Because of further information from the northern basin of England, the Tithonian has the most diverse bivalve fauna in the whole Jurassic, both from the species and the generic aspects. A partially calculated Ryazanian number of species is shown in the figure, but this is incomplete as no information from the 'Berriasian' of the mediterranean has been included. There will not be as great a decrease in the number of species as the graph would suggest. The very large figure of 125 bivalves species in the Tithonian reflects the diverse environments that are represented at this time, varying from quiet-water marine clays, shallow condensed marine sands, shallow marine carbonates, Reefal associations to mesohaline environments (Hartwell Clay, Spilsby Sandstone, Portland Sands, Portland Limestones, Purbeck Beds in England alone). It is interesting to note that although a regressive phase the Tithonian can produce 125 species of 44 genera, while in the transgressive Aptian Lower Greensand Casey (1961) shows 230 species present representing 120 genera in England alone.

6. Renewal Index.

Zakharov and Yanine (1975) used the renewal index (total number of species becoming extinct + total number of new species appearing at a particular horizon) to establish where the greatest rate of species turnover (cf. Hallam 1976) took place in the Jurassic-Cretaceous boundary beds of Boreal bivalve faunas. They conclude that the renewal index is greatest

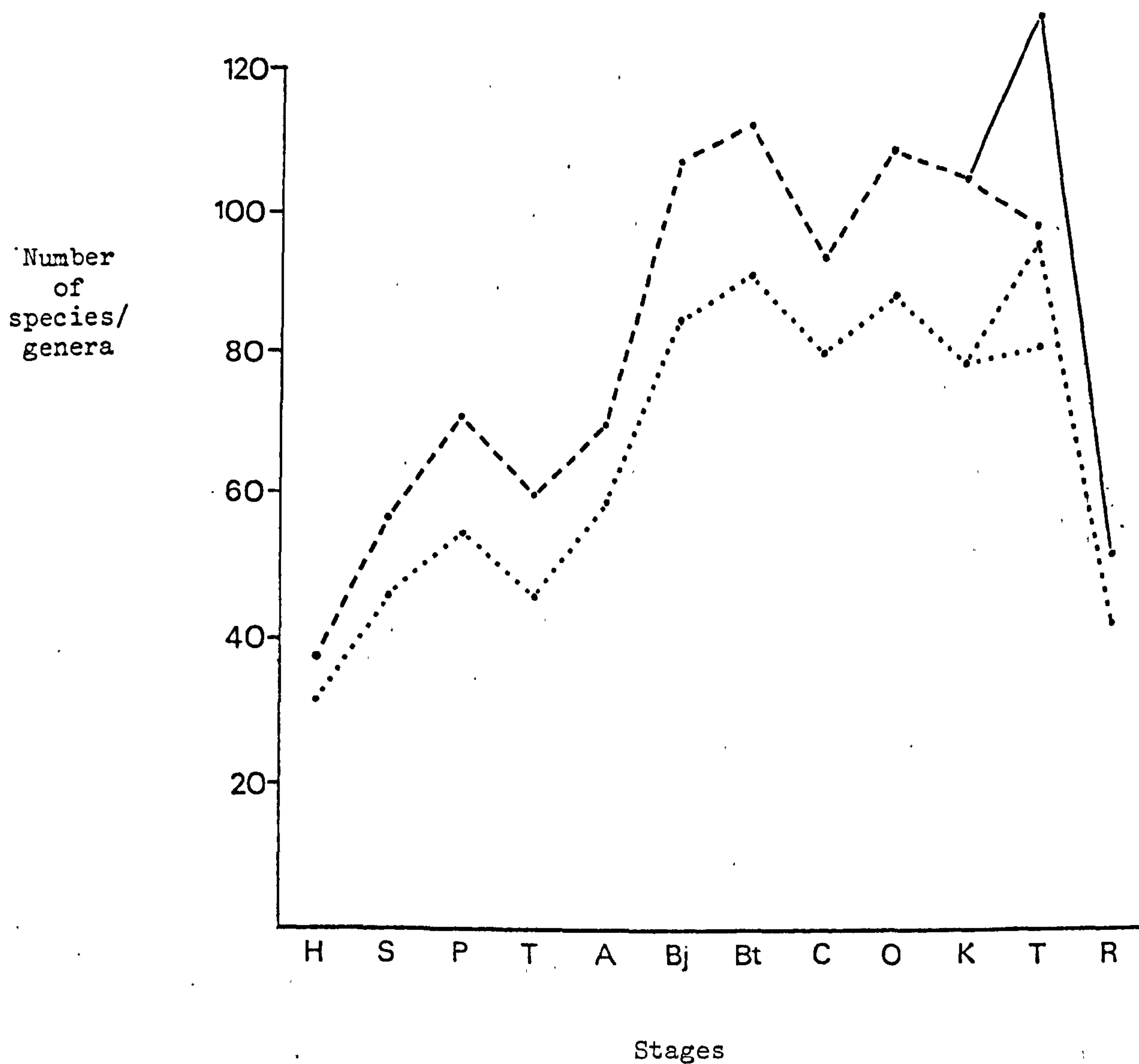


Figure 4.22

Bivalve species and generic diversity in western Europe through the Jurassic into the basal Cretaceous, modified from Hallam (1976). Information for the Ryazanian is plotted from English data only. Stages are indicated by their first letters.

Hallam (1976)	Modified
----- Species	----- Species
..... Genera	----- Genera

in high stress areas, i.e. shallow marine regions, and lowest in deeper water. The Jurassic-Cretaceous boundary itself is not distinguished by significant global faunal change, but by varying degrees of extinction and appearance in different areas.

In eastern England the renewal index is listed below for species appearance and extinction at zonal level. There is no satisfactory information available yet from the Lower Volgian and Valanginian in the region to extend the data into these stages to indicate the change in species with major change in environment.

Zone	Appearance	Extinction	Renewal Index
<u>P. albidum</u>			
<u>S. stenomphalus</u>	7	8.5	13.5
<u>S. icenii</u>	1.5	1	2.5
<u>H. kochi</u>	0.5	8	8.5
<u>R. runctoni</u>	8	1	9
<u>S. lamplughi</u>	5	0.5	5.5
<u>S. preplicomphalus</u>	6.5	7	13.5
<u>S. primitivus</u>	10	0	10
<u>P. oppressus</u>	2	7	9
<u>T. giganteus</u>	12	15	27

The greatest change appears at the junction between the T. giganteus Zone fauna and that of the P. oppressus Zone. The T. giganteus Zone fauna could be condensed from several zones, although there is a possibility that this figure reflects stabilising of the fauna after rapid development to occupy the shallow marine environment which developed in eastern England after the Kimmeridge Clay. It is estimated here that the renewal index

at the base of the T. giganteus Zone in eastern England is probably much larger (40+) reflecting the change from the quiet water bituminous shales of the Kimmeridge Clay. The figures for the renewal index from the Middle Volgian to the Ryazanian inclusive in eastern England are moderately uniform and low (2.5 - 13.5). Even the changes from sandy to clay ironstone facies do not reflect significantly in the figures.

7. Important elements of the Bivalve fauna.

Some taxa appear very frequently within most assemblages studied in the Spilsby basin e.g. Neocrassina (Lyapinella). Although not necessarily dominating the individual assemblages, such taxa may often comprise a significant proportion of the trophic nucleus. If one ranks the order of taxon abundance of the first ten taxa in each assemblage studied (modified from Fager 1957) and gives the most abundant taxon a value of 10 and the least a value of 1, and then add up the values obtained for each taxon, one achieves an indication of the relative importance of the most commonly appearing taxa. The ten most abundant taxa in the Middle Volgian to Ryazanian of the Spilsby basin are as follows:-

1. Neocrassina (Lyapinella)
2. Pleuromya --
3. Entolium---
4. Myophorella -
5. Anisocardia
6. Discoloripes
7. Protocardia
8. Dicranodonta
9. Corbicella
10. Camptonectes

the list brings out the importance of such genera as Myophorella, Anisocardia, Discoloripes, Corbicella and Camptonectes which would normally go unremarked as they never dominate individual assemblages. The forms which do dominate assemblages and also occur as prominent members of other assemblages are naturally best represented, e.g. N. (Lyapinella) and Pleuromya. Entolium and Protocardia are relatively restricted in abundance to their own assemblages.

8. Biofacies Synthesis.

Figure 4.23 is an attempt to give a generalised reconstruction of the biofacies relationships in the Spilsby Basin and also part of the adjacent Speeton Basin during Middle Volgian to Ryazanian times. In the Spilsby Basin the sediments are commonly glauconitic and may contain common phosphatised nodule layers. The faunas appear to be fully marine and the region is envisaged as a shallow shelf area of condensed sedimentation with proximity to land in the south on account of the prominence of lignite especially in the Norfolk area.

The Kimmeridge Clay is overlain unconformably by a condensed horizon of Middle Volgian age from Buckinghamshire to Yorkshire. The condensed horizon is composed of phosphatised nodules and at Nettleton this is associated with a very diverse fauna of the Pleuromya-Grammatodon assemblage. Elements of this assemblage are known from Bedfordshire, the Wash area and Yorkshire but in these latter areas there has been considerable reworking of the horizon and the fauna has been largely destroyed. This is followed generally by silty and clayey glauconitic sands with N. (Lyapinella). This facies generally thins from the south to the north, and locally may

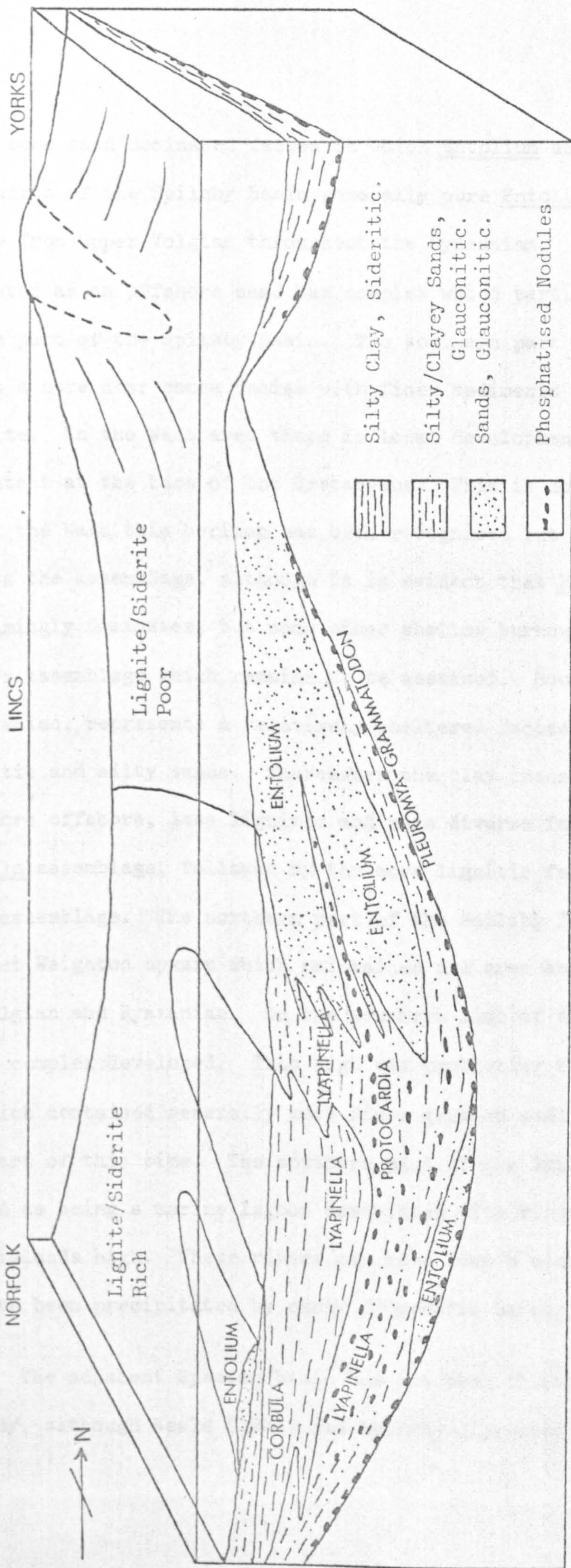


Figure 4.23

Generalised Biofacies distribution in the Spilsby and Yorkshire Basins. Bivalve names indicate the distribution of the principal bivalve assemblages. Not to scale.

contain some sand dominated facies in which Entolium assemblage appears. In the north of the Spilsby Basin generally pure Entolium dominated sands continue from Upper Volgian throughout the Ryazanian. This facies is interpreted as an offshore sand bar complex which partially protects the southern part of the Spilsby Basin. The southern part of the Spilsby Basin develops a more near shore facies with finer sediments and common occurrence of lignite. In the Wash area there is local development of a sand with low clay content at the base of the Cretaceous. This is dominated by Protocardia. North of the Wash this horizon has been recognised but never sampled adequately to assess the assemblage, although it is evident that Protocardia no longer overwhelmingly dominates, but some other shallow burrowing form may indicate a further assemblage which remains to be assessed. South of the Wash during the Ryazanian, represents a relatively sheltered facies with initially glauconitic and silty sands. Thereafter the clay ironstone facies develops with a more offshore, less lignitic and more diverse fauna initially with Lyapinella assemblage, followed by the more lignitic facies with less diverse Corbula assemblage. The northern part of the Spilsby Basin is bounded by the Market Weighton upwarp which maintained the area as a high during the Upper Volgian and Ryazanian. On the southern limb of the upwarp the offshore sand bar complex developed. This high was protecting the southern Spilsby Basin which contained generally much finer grained sediments during the latter part of this time. The southern part of the Spilsby Basin is envisaged as being a marine lagoon associated with rivers draining the London Midlands high. These rivers may have been a source of iron which could have been precipitated by early diagenetic bacterial action.

The adjacent Speeton basin has not been thoroughly examined in this study, although Neale (1968) has briefly discussed the Ryazanian and

Valanginian bivalves. After the initial Coprolite bed of the Speeton Clay, which is probably a conglomerate of phosphatised Middle Volgian material, the clays immediately above indicate a restricted marine environment. The belemnites indicate the age of these clays (D8-D5) to be Ryazanian (Pinckney and Rawson 1974), though ammonites first appear in D7E (Neale, 1962). The benthonic macrofauna of these beds is generally sparse. However some bivalves are recorded from D6 by Neale (1968) and from my own records in Appendix 1. This fauna has not been collected in sufficient numbers for a quantitative study and no assemblage is erected. Neale recognised an initial transgressive phase ending in mid D7 with shallow marine conditions until the end of D6 after which the sea became shallower and more lagoonal with a Lingula fauna. It is believed that the Speeton basin was bounded to the north by the Mid North Sea High, which could have been emergent. To the south lay the Market Weighton axis. These highs partially enclosed the Speeton basin and the absence of coarse clastics suggests that there were no rivers supplying coarse sediment to the basin. Although Parker (1974) shows that the Ryazanian Clays have a high kaolinite to illite ratio, he does not indicate source regions for the sediment. The clays were deposited in a shallow marine environment with a slightly fluctuating sea level. The relatively sparse benthonic macrofauna indicates a probable poor circulation and inadequate food supply to support bottom living forms. Even deposit feeders do not appear well represented by skeletal types although Neale (1968) has indicated that there is a high organic content. Connections to the Spilsby basin were presumably around the Market Weighton axis. It is not possible to discuss the facies changes in the present offshore area as the time control on the limited sections that are available is not as accurate as on land, and the bivalve faunas are unknown. However it is

likely that the mid North Sea high was emergent to the north of the Yorkshire basin and provided a partially enclosing barrier.

9. The Anglo-Paris Basin.

To conclude the discussion of the ecology of the Spilsby bivalves, an attempt is made to compare the fauna to those of contemporary strata in the Anglo-Paris Basin. The discussion centers around figures 4.24-26 which suggest palaeogeographic reconstructions for the area between Yorkshire and north France in the Middle Volgian, the Upper Volgian and the Ryazanian respectively.

In the Middle Volgian (Figure 4.24), the western margins of the figure correspond approximately to the limits of outcrop. The late Jurassic shore line skirts the emergent London-Brabant Massif and an embayment embraces northern France. In central England, the Middle Volgian is represented by glauconitic clays (e.g. Hartwell Clay) and sandy glauconitic limestone (Portland Beds) which appear to have been deposited in the marginal areas of the Anglo-Paris basin. These facies continue under the Weald to northern France. The glauconitic clay facies do not generally have well developed phosphatised hard grounds and the fauna is therefore dominated by forms adapted to life on soft bottoms (e.g. Pinna, Neocrassina and Hartwellia). The local hardgrounds provided by dead shells are commonly encrusted by oysters and presumably also by byssate forms. The description by Oates (1975) and other faunal lists suggest a close comparison with the faunas from the base of the Spilsby Sandstone and the Sandringham Sands which are clayey/silty sandstones. The glauconitic sandy limestones of central England compare most closely to the similar facies in north France.

The fauna is dominated by Laevitrignia and large Protocardia which are not known in situ in the Spilsby Basin. The fauna is mainly that described by de Loriol (1867, 1875) from Northern France. (See Pruvost and Pringle (1924) for the French stratigraphy and Ager & Wallace (1966; 1970) for discussion of the facies). The Portland Sands of Dorset contain facies such as the Exogyra Beds which are only recognised elsewhere in northern France.

The more offshore upper part of the Kimmeridge Clay in Dorset with common Thracia and lucinids does not compare to eastern England faunas which are contemporary although it may be similar to some parts of the Hauterivian Speeton Clay. The Portland limestones of Dorset again provide contrasting facies to eastern England and were deposited in warmer water with progressive reduction in salinity. The bivalves have been briefly described by Cox (1925, 1929). The progressive removal of inarticulate brachiopods, belemnites, articulate brachiopods, corals and ammonites has been discussed briefly by Ager and Townson (1976).

It is believed here that the critical structure which caused the isolation of southern England from Tetheys is probably the Cottentin-Devon axis (Juignet, Rioult & Destombes, 1973, 322). The axis is believed to have become critical in the late Middle Volgian and remained until the Aptian when it was breached from the west in the Prodeshayesites obsoletus Subzone (Casey 1961b). During the time that the axis was positive, drainage of the Anglo-Paris Basin was to the north across the English Midlands.

In the Upper Volgian (Figure 4.25) southern England is interpreted by West (1975) as being a shallow subtidal to high intertidal gulf area with moderately hypersaline to evaporitic conditions, in which were deposited the Lulworth Beds. This is the culmination of regression in the late Jurassic in the area. The bivalve fauna, partially described by Casey

(1955a, 1955b) contains species of Laevitrignia, Hemicorbula, Corbicellopsis, Eomiodon and Eodonax which provide no comparison to any Spilsby material. Barriers in the Bedford region must have hindered normal marine access to the north.

Casey (1963) recognised the Cinder Bed of Dorset and the ferruginous sands of the western outliers, later described as the Whitchurch Sands (Casey and Bristow, 1964), as representing the basal Ryazanian transgression in southern England (Figure 4.26). Casey (1962) postulated a northern source for the marine influx in to the southern basins and this has been maintained by subsequent workers (e.g. Kaye, 1965). Casey and Bristow (1964) have already indicated the faunal diversity decrease from central England southwards into Dorset. The Whitchurch Sands contain a fauna of small bivalves including Protocardia, Corbula spp. and Laevitrignia. Ammonites have not been recorded. The salinity was presumably reduced. In the Vale of Wardour Liostrea, Laevitrignia and Myrene occur commonly, but of note is the rare Myophorella densinoda (Etheridge) which is exceptionally similar to the Upper Volgian M. tealbyensis from Lincolnshire from which it has almost certainly evolved again indicating a northern connection to open sea. In Dorset the bivalve fauna is virtually restricted to Liostrea which forms the lumachelle of the Cinder Bed horizon. Later in the Durlston Beds of Dorset fresh and brackish water conditions are recognised with Viviparus and Unio which herald the Wealden environment of southern England. In eastern England the facies remained marine throughout the Ryazanian, but there is indication of weak regression giving a slightly more restricted environment in the upper part of the Mintlyn Beds and in part of the Speeton Clay. In central and southern England the change is paralleled but more extreme in the change from marine to fresh water conditions.

MIDDLE VOLGIAN

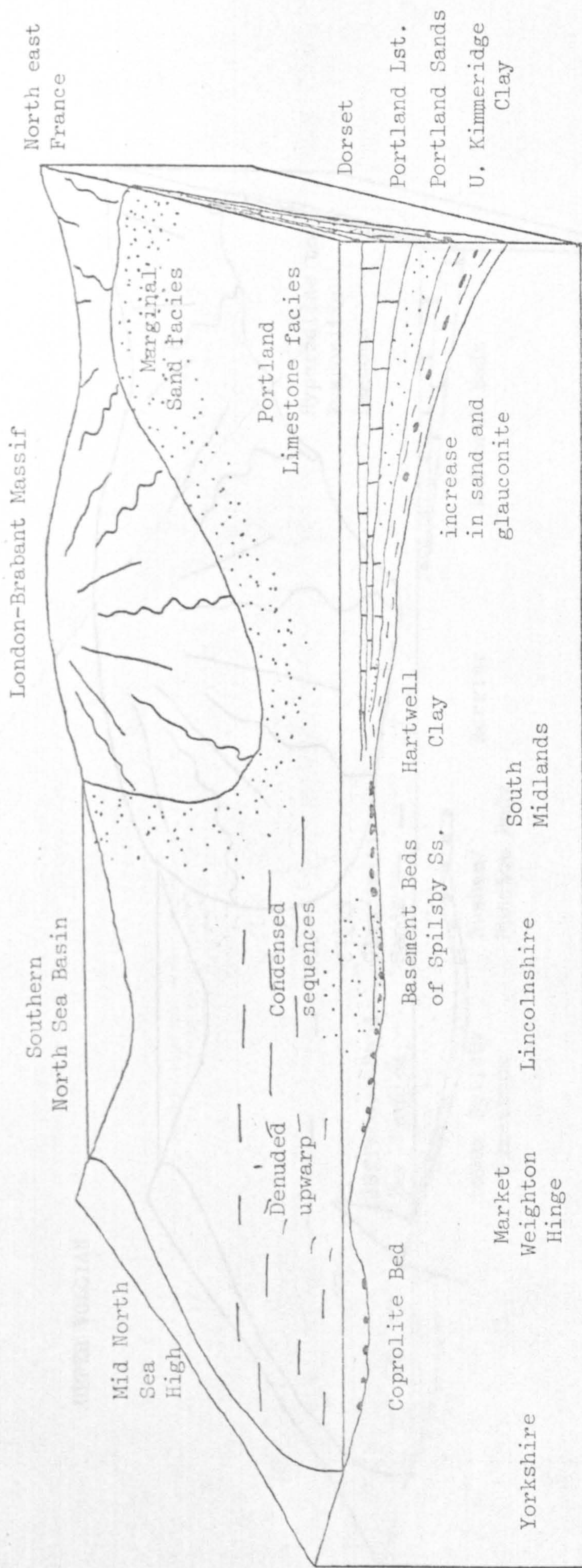


Figure 4.24

Middle Volgian Palaeogeography of eastern and southern England and north east France.

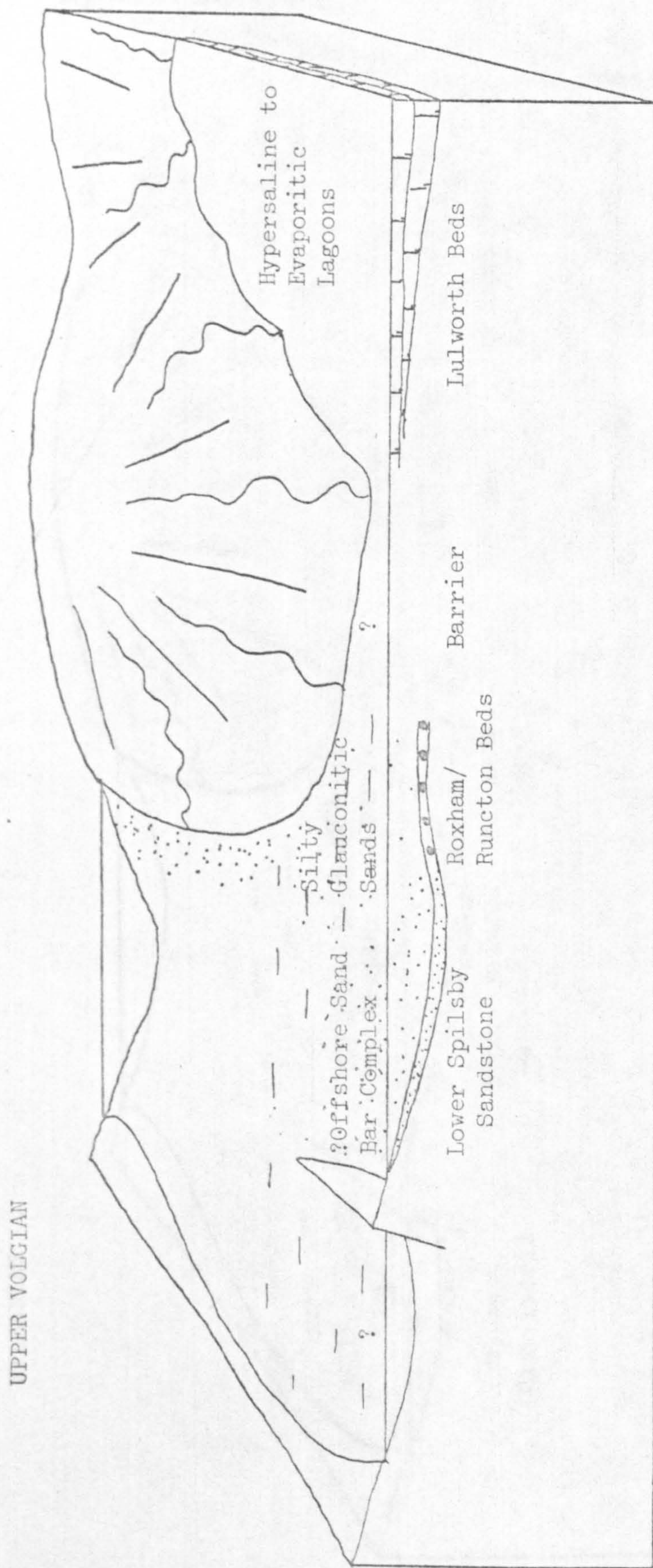


Figure 4.25

Upper Volgian Palaeogeography of eastern and southern England and north eastern France.

RYAZANIAN

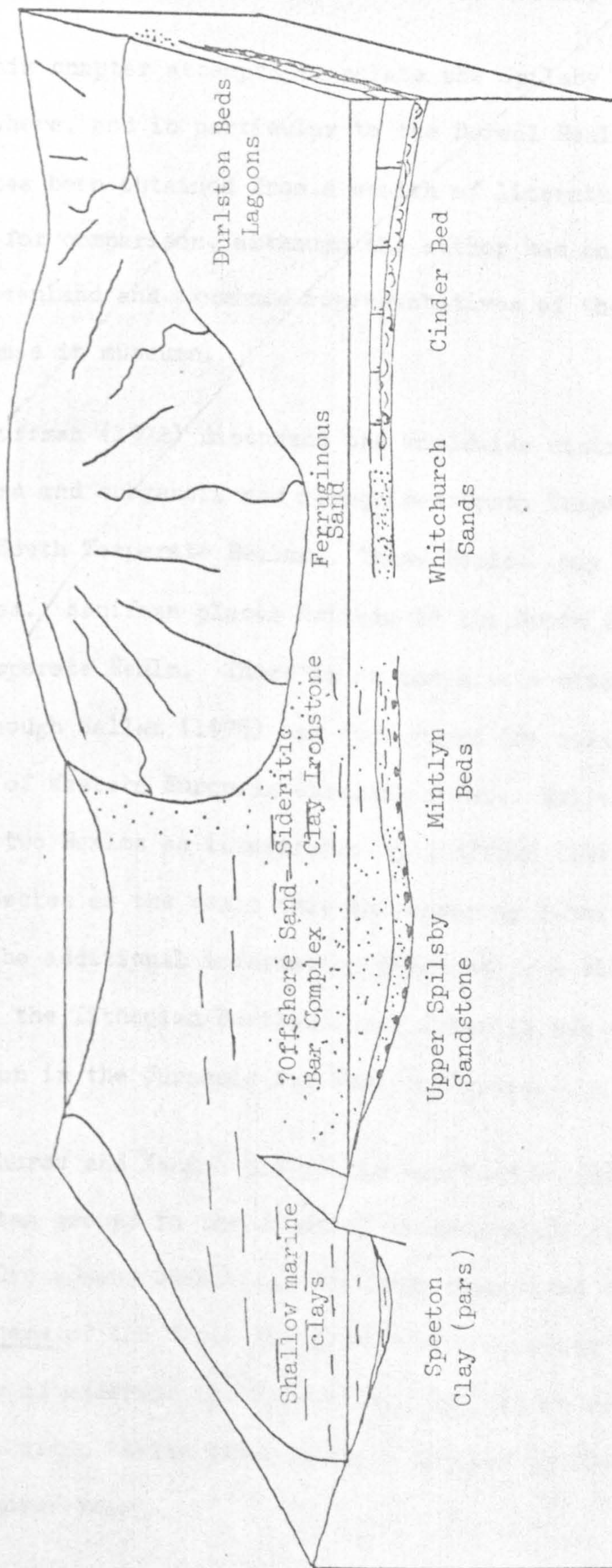


Figure 4.26

Ryazanian Palaeogeography of eastern and southern England and north east France.

Chapter 5. GEOGRAPHICAL DISTRIBUTION OF THE SPILSBY FAUNA.

This chapter attempts to relate the Spilsby bivalve fauna to faunas elsewhere, and in particular to the Boreal Realm. Information for this study has been obtained from a wealth of literature, principally using photographs for comparison, although the author has collected specimens from East Greenland and examined representatives of the European and Russian Platform faunas in museums.

Kauffman (1972) discussed the worldwide distribution of Cretaceous bivalve genera and subgenera and recognised North Temperate (=Boreal), Tethyan and South Temperate Realms. These Realms may be further subdivided into Provinces. Kauffman places Britain in the North European Province of the North Temperate Realm. There is no comparable study for the Jurassic bivalves although Hallam (1976) has summarised the stratigraphical distribution of Western European Jurassic forms. Hallam's study spans provinces in two Realms as interpreted by Kauffman (1972). Hallam preferred to use the species as the basic unit in comparing bivalve diversity with time. With the additional information obtained from the present study, it is clear that the Tithonian/Portlandian/Volgian is the climax of bivalve diversification in the Jurassic for Western Europe.

Zakharov and Yanine (1975) and Kauffman (1972) recognise endemic and cosmopolitan groups in the study of biogeographic provinces in late Jurassic and Cretaceous bivalves. Kauffman recognised c28% endemism in Berriasian genera of the North European Province, which represents a fauna during a phase of moderate transgression. The figure remained approximately constant until after Albian times when it dropped to 10-15% during a widespread transgression.

In eastern England, endemic percentages, calculated here on species are

Middle Volgian	15.6%
Upper Volgian	16.2
Ryazanian	20.9

In comparison, the Portland Beds (Middle Volgian) of southern England have about 50% species endemism, calculated from the faunal list of Cox (1929). Furthermore, in direct comparison to these figures are those calculated by Zakharov and Yanine (1975, fig. 5) which are reproduced below:

	Volgian	Berriasian
North Siberia	46%	38
North Urals	17	7
East Greenland	3	10
California	27	23
East Europe	36	20

Hence it appears that endemism is highest in shallow marine basins that are partially enclosed and with only one access channel to other marine areas, eg. the Wessex basin (Middle Volgian) in north west Europe and in the Volgian and Ryazanian of North Siberia. Regions such as East Greenland are marginal to major channels and will have low endemism because of faunal mixing due to marine currents.

Zakharov (1972 in Saks Ed.) summarised Boreal bivalve distributions at the Jurassic-Cretaceous boundary. He concluded that:

1. The species level was the most significant for understanding bivalve complexes.
2. Facies distribution affected both temporal and spacial distribution of bivalves.
3. Some bivalves span the Jurassic-Cretaceous boundary beds, while others evolve through it.
4. The greatest rate of turnover takes place generally within the Ryazanian and not at its base.
5. The Ryazanian bivalve fauna is more similar to that of the Valanginian and not to the Volgian.

Although Kauffman has made the genus and subgenus the basis of his global work, it is believed here that the species is the best unit for direct comparison especially in studying moderately close geographic regions. Some genera may be cosmopolitan, although some species of those genera may be distinctly endemic. Therefore in using the generic level there may be some blurring of the boundaries between provinces.

The Spilsby fauna is compared below with other regions: the most closely related areas are Boreal. The overlap of the faunas of these other regions with the Spilsby fauna is summarised in figure 5.1a-c,

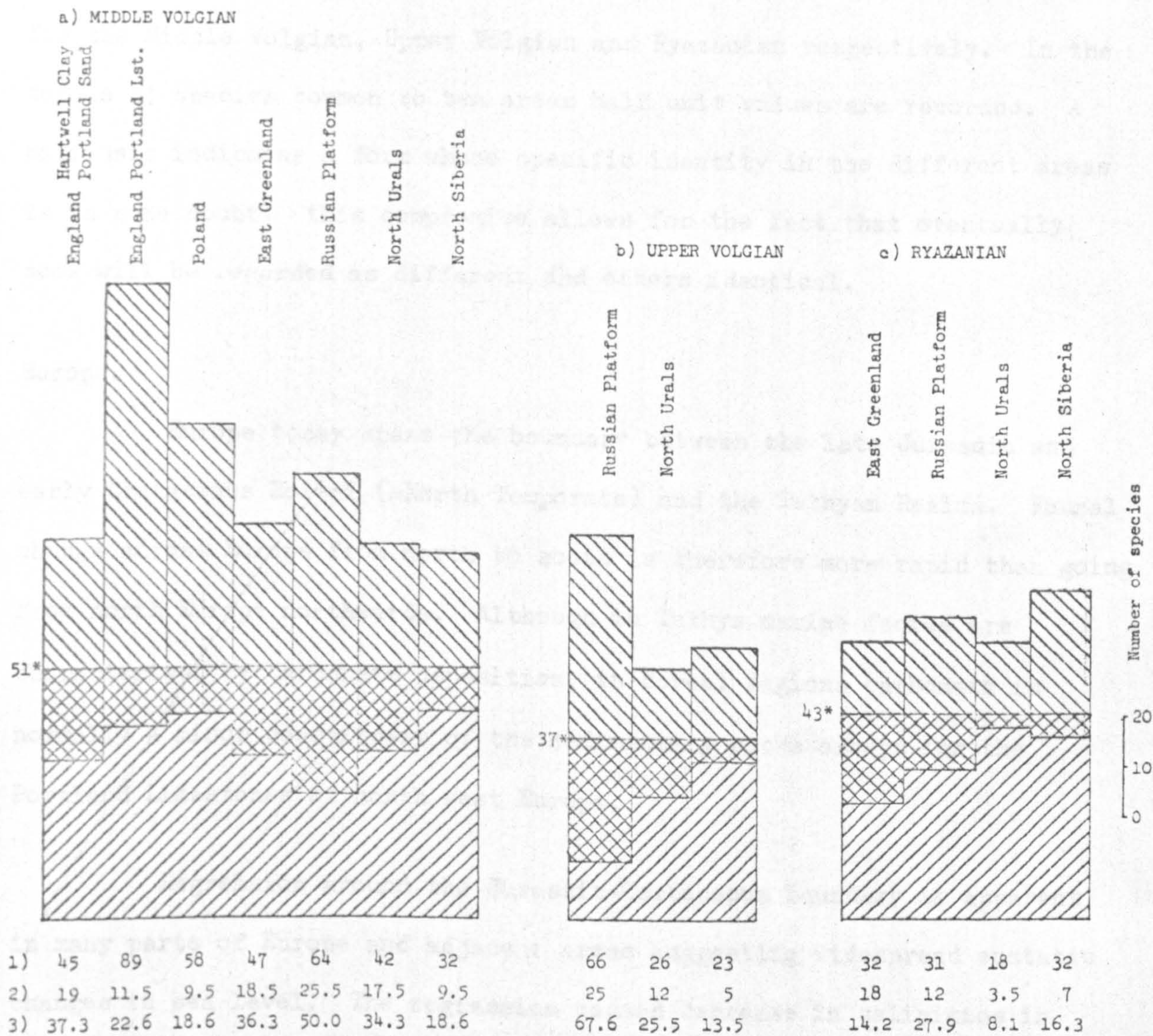


Figure 5.1

Species overlap figures showing the proportional distribution of the Spilsby bivalves in relation to the principal described bivalve faunas of Boreal regions in a) the Middle Volgian, b) the Upper Volgian and c) the Ryazanian. The number of Spilsby species recorded in each stage of substage is indicated thus: *. Row 1) is the total number of alien species recorded. Row 2) is the total number of alien species present in the Spilsby fauna. Row 3) is the % of Spilsby fauna composed of species which also occur in the other areas.



Spilsby Species



Alien Species

for the Middle Volgian, Upper Volgian and Ryazanian respectively. In the totals of species common to two areas half unit values are recorded. A half unit indicates a form whose specific identity in the different areas is in some doubt: this compromise allows for the fact that eventually some will be regarded as different and others identical.

Europe.

Europe today spans the boundary between the late Jurassic and early Cretaceous Boreal (=North Temperate) and the Tethyan Realms. Faunal change across Europe from north to south is therefore more rapid than going from north Europe northwards. Although in Tethys marine facies are characterised by carbonate deposition, in Boreal regions carbonate is normally a minor constituent of the sedimentary rocks except for the Portland Limestones of north west Europe.

Regression around the Jurassic-Cretaceous boundary is apparent in many parts of Europe and adjacent areas suggesting widespread eustatic changes in sea level. The regression caused decrease in salinities in formerly shallow marine basins which is recognisable in the bivalve faunas. In central Europe this regression can be seen in the Haute Marne (de Loriol 1872), the Jura (de Loriol and Jaccard 1865) and Bavaria (Wellnhofer 1964; Barthel 1969).

Also in south east Europe Tethyan facies occur with practically no overlap of bivalve species with Boreal forms. Such facies include the Upper Tithonian rudistid reefs of Czechoslovakia (Blashke 1911). Further east, Tethyan faunas are recorded from the Caucasus (Sakharov 1975), the Crimea (Drushchits 1975) and Mangyuyschlak (Saveliev 1958; Louppov, Bogdanova and Lobatcheva 1975). A notable exception is the occasional presence in

Stage	LOWER VOLGIAN			MIDDLE VOLGIAN						UPPER VOLGIAN			RYAZANIAN			
	Region			Region						Region			Region			
Taxa	1 North west Europe	2 Bavaria	3 North Urals	4 Eastern England	5 North west Europe, clay/sand	6 North west Europe, limestone	7 Poland	8 East Greenland	9 Russian Platform	10 North Urals	11 North Siberia	12 Eastern England	13 East Greenland,	14 Russian Platform	15 North Urals	16 North Siberia
<u>Nuculoma variabilis</u>	x				x											
<u>Parbatia cf. mysis</u>		o		x		o									x	x
<u>Grammatodon schourovskii</u>			x	x	x			x	x							
" <u>spilsbiensis</u>												x				
" <u>compressiusculum</u>			x	x	x				x							
" <u>productum</u>		o						x	x							
<u>Cucullaea varans</u>				x								x				
" <u>benniworthensis</u>												x		x		
<u>Musculus fischerianus</u>				x					x			x				
<u>Modiolus sibiricus</u>				x								x				
" <u>aff. vicinalis</u>				x			o		o			x			o	
<u>Falciavtilus suprajurensis</u>				x		x				x		x				
<u>Pinna suprajurensis</u>							o	x		x	o	x				
" <u>cf. constantini</u>	o	o		x	x				o			x				
" <u>aff. subcuneata</u>												x				
<u>Arpaea brachowi</u>												x				
" <u>sphenoides</u>												x				
<u>Isognomon aff. cuneatum</u>				x	o	o	o	x				x				
<u>Malletia sp.</u>												o				
<u>Oxytoma octavia</u>		x		x	x	x	o	x	x	x	x	x	x	x	x	x
<u>Arctotis intermedia</u>				x								x				
<u>Entolium orbiculare</u>	x	x	x					x		x	x	x	x	x	x	x
<u>Camptonectes morini</u>	x	x	x	x	x			x		x	x	x	x	x		o
" <u>cinctus</u>		o						o		o	o	x			x	x
" <u>cf. intertextus</u>				x												
<u>Buchia rugosa</u>				x	x		o	x	x	x						
" <u>volgensis</u>															x	o
<u>Plicatula producta</u>				x	x	o		x				x				
<u>Placunopsis distracta</u>				x	x	o		x	x		x	x				x
<u>Pseudolimea arctica</u>				x				x	x	o	x	x			o	x
<u>Linea bodylevskii</u>			x									x				
<u>Plagiostoma planicosta</u>				x												x
" <u>subtrigida</u>			o							o	o				x	
" <u>sp.</u>	o			x	o										x	
<u>Liostrea plastica</u>	x	x		x	x		x	x	x	x	x					
? " <u>extensa</u>				o		o	x		o			o			o	
<u>Nanogyra thurmanni</u>	x			x	x	x	x		o			x			x	o
<u>Iotricopia borealis</u>				o	o							o			x	x
<u>Myophorella intermedia</u>				x			x	x	x			x				
" <u>tealbyensis</u>												x				
" <u>atlantica</u>															x	x
" <u>claxbiensis</u>															x	
<u>Codakia? cf. crassa</u>				x												
<u>Mesonoltha? kostromensis</u>		o		x								x				
<u>Discoloripes septentrionalis</u>								x	x			x			o	x
" <u>fischerianus</u>		o							x			x				
" <u>cf. inaequalis</u>				x				o								
<u>Myoconcha cf. northlandica</u>	o	o			o	o	o					x				
<u>Neocrassina asiatica</u>				o					x	x	x	x			x	x
" <u>groenlandica</u>															x	x
" <u>laevis</u>															x	
" <u>pelops</u>				x	o					o	o					
" <u>woldai</u>				x								x			o	

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<u>Nicaniella mnewnikensis</u>				x	o				x					x			o				
" <u>claxbiensis</u>				x								x					x				
<u>Protocardia concinna</u>			x						x	x		x		x	x		x	x	x		
<u>Senis aff. petschorae</u>				x						x					x		x				
<u>Sowerbya longior</u>	x				x	x						x					x				
<u>Corbicellopsis claxbiensis</u>	o				x			x				x					x	x			
<u>Anisocardia lincolnshirensis</u>				x																	
" <u>sandringhamensis</u>				x													x				
<u>Hartwellia hartwellensis</u>	x			x	x							x									
" <u>mintlyni</u>																	x	o			
" <u>cancriniana</u>				x					x	x				x	x				x		
<u>Procyprina centralis</u>												x					x				
<u>Hiatella foetida</u>				x	x																
<u>Martesia constricta</u>																	x				
<u>Pholadomya interrupta</u>	o		o	x	o			x	x	x	o	x			x						
" <u>mediana</u>											o						x				
" <u>aff spectonensis</u>				x																	
<u>Goniomya rawsoni</u>								x	x	x		x		x			o	o			
<u>Girardotia compressa</u>			x	x						x	x										
" <u>wrighti</u>																	x				
<u>Cresslya cf. alduini</u>				x					x	x				x	x				x		
<u>Pleuromya orbignyana</u>							x		x			x		x					x		
" <u>spilsbiensis</u>				x																	
" <u>cf. uniformis</u>	x			x	o	x	x	x	x	x		x		x			x	x	x		
<u>Thracia depressa</u>	x		x	x	x	x	x	x	x			x		x			o				
" <u>phillipsi</u>																	x				

Figure 5.2

Distribution of the Spilsby bivalves with relation to time and to other Boreal areas, based upon comparison with the following literature, Blake 1880, Cox 1929, Gerasimov 1955, 1969, Lewinski 1923-1924, Sanin 1976, Spath 1936, 1947, Zakharov 1966, 1970 and Zakharov & Mezesnikov 1975. x signifies a high level in confidence of specific identity with the Spilsby fauna and o a low level of confidence.

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quantity of Buchia in the eastern European areas.

Northern Europe represents the southern edge of the South North Sea basin, and provides contrasting facies and faunas to southern Europe. Regressive facies appear again and Huckreide (1967) has described the molluscan faunas of the brackish and fresh water facies of northern West Germany. In the Spilsby basin, however, although there was shallowing from Kimmeridgian to Volgian, the area remained fully marine and brackish and freshwater faunas are not known. Elsewhere in the Southern North Sea Basin marine bivalve faunas have only been recovered from Denmark, where rich molluscan assemblages have been obtained from the Hirshals erratic boulders which were described by Skeat and Madsen (1898). Some of this fauna could be Middle Volgian in age, although much appears to be Lower Volgian and is more closely comparable to the Shotover Grit Sands of south central England. From boreholes, Sorgenfrei and Buch (1964) figured Buchia volgensis which suggest a Ryazanian age for some strata. Although this information is incomplete, there could be a high degree of correlation between the eastern England and Danish faunas.

In Poland there is a late Jurassic regressive sequence with marine to brackish conditions. During the Ryazanian there was a renewed transgression. The fully marine Middle Volgian faunas were described by Lewinski (1923-24) and were collected from limestones. They contain distinctive elements such as plicate ostreids, nuculids, corbids and cucullaeids, which contrast with the contemporary Portland Beds. However 19% of the Spilsby fauna is represented in the Polish Middle Volgian which is slightly less than the 24% calculated for the Portland Beds. Lewinski unfortunately did not give a quantitative account of the fauna, although Dabrowska (1975, 244) believes

that the Polish fauna compares much more closely to the Portland Reds than to the Middle Volgian of the Russian Platform. The marine limestones of the Middle Volgian give way to brackish facies with corbulids in (presumably) the Upper Volgian. The Ryazanian transgression appears to have come from the south with a predominantly Tethyan ammonite fauna. Sandy siltstones, sandstones and sandy limestones, give way to clays. The bivalve fauna has not been examined in detail although Marek (1969) has listed some elements and Pugaczewska (1975) has described the oysters as Rhynchostreon etalloni (Pictet and Campiche) and Ceratostreon tuberculiferum (Koch and Dunker). This fauna is not yet known in sufficient detail for comparison with England.

Russian Platform.

Late Jurassic and early Cretaceous faunas are moderately well known from the Russian platform and Gerasimov (1955, 1969) has summarised and illustrated the molluscan fauna. The Volgian and Ryazanian strata are composed of condensed sequences with glauconitic sands and clays with phosphatised nodule horizons. The correlation with eastern England is fully discussed by Casey (1973) although the completeness of the fossil record has been questioned (Casey 1968, p.65).

The bivalve faunas of the Russian Platform resemble those of eastern England. In the Middle Volgian 50% of the eastern England fauna is composed of species occurring on the Russian Platform; the Upper Volgian figure is 67% and the Ryazanian figure 40%, showing a high degree of correlation. However the proportional representation of species is very different. The principal difference lies in the prominence of Buchia in the Russian Platform faunas, in contrast to its general scarcity in England.

The variety of Buchia species is diverse on the Russian Platform and includes the distinctly narrow forms B. russiensis (Pavlow) and B. tenuicollis (Pavlow) in the Middle and Upper Volgian respectively, species which are not represented in north west Europe. In the Berriasian alone 26 species of Buchia have been recognised by Pojarisskaja (1972); these belong to three subgenera, namely Buchia ss., Pirumcella and Trigonicella, which may represent more natural species groups. Other distinctive Russian Platform species include Neocrassina (Lyapinella) duboisiana (D'Orbigny), Nicaniella? veneris (Eichwald), Coelastarte rouillieri Gerasimov, 'Astarte' (probably Venericyprina) panderi (Rouillier), Opis rouillieri Lahusen and Trigonia suevi Stremouchov. Zakharov (in Saks Ed. 1972) notes a Renewal Index of 18 at the base of the D. panderi Zone, while at the base of the V. virgatus Zone the Index reaches 53. This latter figure is probably close to the size of the Index to be expected at the base of the Basal Spilsby nodule bed. At the base of the Ryazanian the Index is 11 while at the base of the S. spasskensis Zone it rises to 26 and only one species drops out at the base of the Valanginian. The greatest change is therefore in the Middle Volgian, there is moderate change within the Ryazanian and the Valanginian arrives with scarcely any change. This pattern is very close to that of the Spilsby basin.

Most of this information is obtained from the areas in the vicinity of Moscow. In the Petchora basin to the north, borehole information indicates that moderately deep water facies exist with Buchia again as the dominant bivalve.

North Urals.

The stratigraphy and the ammonite and bivalve faunas of the

Volgian of the North Urals have been described recently by Zakharov and Mesezhnikov (1974), while the Berriasian stratigraphy and bivalve fauna have been summarised in Saks (Ed. 1972). Around the Jurassic Cretaceous boundary, the facies are principally shallow marine and frequently iron rich. In these sections mentioned by Zakharov and Mesezhnikov (1974) and in Saks (Ed. 1972) Buchia rarely forms the dominant part of any bivalve assemblage - if so it is in generally fine grained sediments suggestive of deeper or quieter water. Although byssate bivalves may frequently make up the bulk of the bivalve assemblages, only occasionally do they comprise a dominant taxon (eg. Boreionectes). It is much more common to find infaunal elements such as Pleuromya, Panopaea and Cyprina dominating in fine grained sands and Cucullaea and Astarte more prominent in coarser sands.

The Middle Volgian bivalve fauna of eastern England is composed of species occurring in the North Urals; the Upper Volgian figure is 25% and the Ryazanian figure is 8%. The first two figures show a moderately good degree of correlation with eastern England, but the Ryazanian figure is noticeably low. This may reflect an inadequately described Russian fauna. Elements of the North Urals fauna which are distinct from English forms include Aguilerella, Cucullaea sibirica (D'Orbigny), Liostrea gibberosa Zakharov; Astarte lyuliyaensis Zak., A. uralensis Zak., and Tancredia hartzi Cox.

No attempt is made to compare eastern England with Novaya Zemlaya and Spitzbergen as there is as yet no good summary literature on the bivalves. It is clear that Buchia forms a significant part of the faunas (eg. Sokolov and Bodylevsky 1931), but the proportions of other elements of the fauna are not given.

Northern Siberia.

Northern Siberia is here interpreted as being the area between the Yenisei and Lena Rivers, including the principal areas of the Taimyr peninsular and the Khatangsk basin. The systematics of the anisomyarian bivalves of the Jurassic-Cretaceous boundary have been studied by Zakharov (1966) and other contributions include Zakharov (1965) on Boreionectes and Sanin (1976) on Ctenodonts. Zakharov (1972) in Saks Ed.) has summarised the ecology of Ryazanian bivalves. A variety of facies from shallow to moderately deep marine have been recognised in the late Volgian and Ryazanian. In the littoral-marine shallow water facies, two subfacies are recognised, firstly a sandy bottom type and secondly a muddy silty bottom type. The sandy bottom is characterised by thick shelled forms including Boreionectes, Arctica, Tancredia, Astarte and also Modiolus, Aguilerella, Pinna, Parallelodon and Entolium. Buchia is noticeably poorly represented. These are all forms which appear to be adapted to living in relatively high energy conditions and ecologically compare closely to the Spilsby Sandstone faunas. In muddy-silty bottoms Buchia becomes more important and Nucula, small Pinna and small Astarte become significant elements of the fauna. In the middle part of the sublittoral marine facies of moderate depths clayey silts and clays are found. Small Prorokia and Buchia are the typical elements of the bivalve fauna. In the lower sublittoral facies of relatively deep water, clays predominate. Benthonic bivalve assemblages are dominated by Buchia and thin shelled pectinids, while Limatula, Oxytoma and Nucula are second order members of assemblages.

In Middle Volgian the Spilsby fauna contains 19% of the Middle Volgian Spilsby fauna is composed of Siberian species, 14% in the Upper Volgian and 17% in the Ryazanian indicating only

a moderate degree of overlap of the faunas. The reasons for this, include the high degree of endemism in northern Siberia which was a large partially enclosed basin throughout Jurassic-Cretaceous boundary times and the geographical separation of the areas. Typical taxa excluded from England include a wealth of Buchia species, Aguilerella, Aequipecten, Cucullaea arctica, and Anabarella.

East Greenland.

Jurassic-Cretaceous boundary beds in East Greenland are beginning to be well described (eg. Surlyk et al. 1973). Ammonite faunas are partially described (eg. Spath 1936, 1947, 1952; Donovan 1964; Surlyk 1972). However bivalve faunas are incompletely known. Spath (1936) has described a rich fauna principally of Middle Volgian age from Milne Land, and a Ryazanian fauna from Southern Jameson Land (1947) while other small contributions have been made by Madsen (1904) and Ravn (1911). I have examined collections in the Greenland Geological Survey and it is clear that further bivalve faunas exist of Upper Volgian age in Southern Jameson Land, and to the north there are further undescribed faunas from Wollaston Forland. Furthermore I have made small collections in the Ryazanian of Southern Jameson Land.

The Middle Volgian bivalve fauna from the Glauconitic Series of Milne Land, described by Spath (1936), is not dominated by Buchia although B. mosquensis and B. rugosa occur. Common byssate bivalves include Isoemmon, Pinna and Modiolus. Shallow burrowing forms are generally thick shelled eg. lucinids and N. (Lyapinella) while the normal deep burrowing forms with thin shells are also common (Pleuromya and Pholadomya). This appears to represent a relatively unstable subtidal sandy environment,

where there is frequent current reworking of the top few centimetres of sediment. No detailed faunal composition has been established but it may correspond to somewhere between a Lyapinella and Entolium assemblage. 36% of the Middle Volgian bivalve fauna of eastern England is composed of species also occurring in Milne Land.

During the 1973 Jameson Land Expedition three principal facies in the Ryazanian were examined. In the micaceous silty shales of the Crinoidbjerg Member of the Hesteelv Formation occasional Nuculoma, Protocardia and crinoid debris were found associated with Hectoroceras, which suggests a quiet water offshore facies of moderate depth with deposit feeders and shallow burrowing bivalves. This facies is not represented in eastern England, but appears to be similar to some of the quieter water facies described in the Ryazanian of northern Siberia (in Saks Ed. 1972). The second facies examined was the basal conglomerate of the Muslingeelv Member, in which the ammonite Hectoroceras is common and Bojarkia is occasionally found. It is a micaceous sandstone and intraformational conglomerate. Buchia is the most common bivalve, but it is almost always disarticulated. N. (Lyapinella) and Lucina spp. are well represented, but only the shells of the latter are found frequently articulated. Nuculids are common but disarticulated suggesting nearby environment suitable for deposit feeders. Otherwise the bivalve shells are highly disarticulated and current sorted (See Surlyk, 1972, fig. 10). The accumulation therefore appears to be largely displaced. Finally a further conglomerate which is considerably ironstained occurs with the ammonites Surites and Phylloceras. In this conglomerate Buchia is again common but almost always with disarticulated valves. Other common elements include Protocardia, Oxytoma and cucullaids but the fauna again is likely

to have been transported in part at least from quieter water environments. Despite the marked facies differences between eastern England and East Greenland, 41% of the eastern England fauna in the Ryazanian is composed of species occurring in East Greenland. The general high degree of correlation between England and Greenland at this time indicates that open seaway directly connected the two areas, which in pre-drift terms would have been only c1500 km apart. Significantly different elements of the Greenland fauna include Buchia okensis (Pavlow), Plagiostoma incrassata (Eichwald), 'Lucina' spp., Tancredia hartzi Spath and Hartwellia groenlandica (Spath).

It should be noted that Buchia is important as a stratigraphic indicator in North America and the Soviet Union, but despite its abundance in East Greenland it has not been studied closely, though several specimens have been figured and Jeletzky (1973) has used it for correlation between Greenland and Arctic Canada.

North America.

In North America there are two principal marine biotic provinces recognised in the late Jurassic and early Lower Cretaceous. A North American Boreal province extended across the Canadian arctic archipelago into northern Alaska, and a North Pacific province stretched from South Alaska southward along the west American coast (Jeletzky, 1971, fig. 3). Buchia clearly transgressed the boundary between the provinces and reached as far south as Mexico. The boundary is recognised principally from ammonites and is not fixed through time but tends to migrate northwards and southwards depending on the prevailing conditions (Jones, 1973;

Rawson, 1973). Buchia is the most important bivalve in America and has been studied stratigraphically (Imlay 1959) and used for mapping (Jones, Bailey and Imlay 1969). Jeletzky (1965, fig. 3) provides a useful summary of the distribution of Buchia showing that in Upper Jurassic and Lower Berriasian times, the Buchia faunas of the North Pacific and Arctic Faunal Realms were homogeneous but that in the Upper Berriasian the two areas developed their own specialised faunas. Only in the late Valanginian did faunas blend again. The sequence of Buchia faunas of East Greenland, and as far as is known the scant faunas of the British Isles correspond closely to those of Arctic Canada. Other bivalves in North America are not well known, and the stratigraphic reliability of some of the literature (eg. Anderson 1938, 1945) is doubtful, therefore I have not attempted to make correlation with eastern England.

Conclusions.

The Spilsby bivalve fauna compares most closely with the contemporary faunas of East Greenland and the Russian Platform. The proportion of the Spilsby fauna contained in other areas drops with distance towards the east and the north east. To the west no contemporary faunas are known and to the south (Tethys) they are markedly different. The fauna is therefore distinctly Boreal. Within Britain the Spilsby fauna does not compare closely with that of the Portland Limestone facies, although there are strong similarities with the Shotover Grit Sands (Lower Volgian) and Hartwell Clay (Middle Volgian) faunas.

The geographic distribution of some important Spilsby and other Boreal taxa is shown in Figures 5.2 - 5.5. An attempt is made to contrast the endemic species eg. Myophorella tealbyensis with more widespread types eg. Neocrassina asiatica and N. duboisiana. Taxa that are widespread

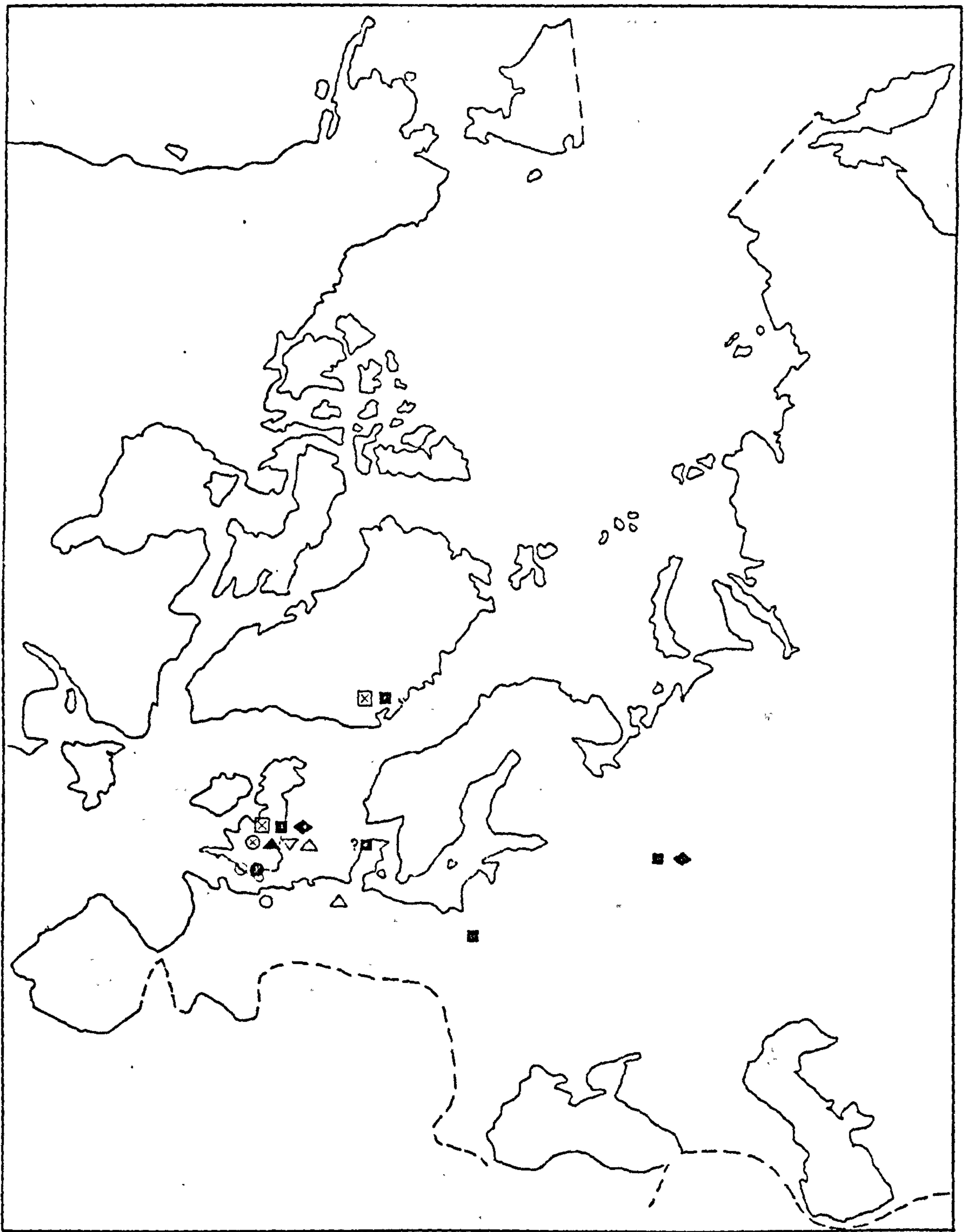


Figure 5.3

Geographic Distribution of the Spilsby Trigoniidae.

<u>Iotrigoia atlantica</u>	Ryazanian	⊠
<u>Myophorella intermedia</u>	Middle Volgian	■
<u>Myophorella intermedia</u>	Upper Volgian	◆
<u>Myophorella tealbyensis</u>	Upper Volgian	⊗
<u>Myophorella keepingi</u>	Ryazanian	▲
<u>Myophorella claxbiensis</u>	Ryazanian	▼
<u>Myophorella claxbiensis</u>	Valanginian	△
<u>Laevitrigoia spp</u>	Middle Volgian	○
<u>Laevitrigoia spp.</u>	Ryazanian	●

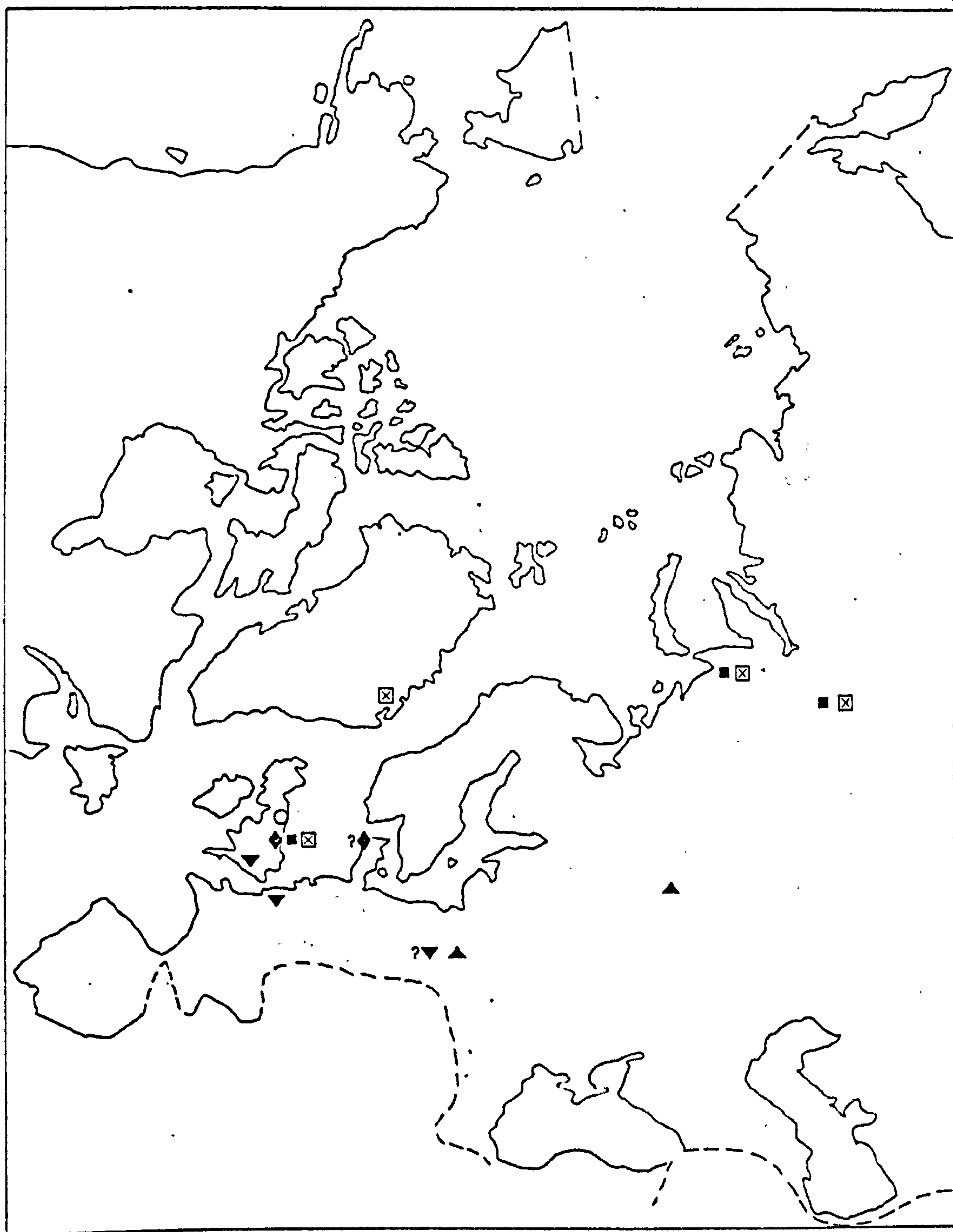


Figure 5.4

Geographic distribution of Spilsby Neocrassina (Lyapinella) and related species.

<u>N. (L.) saemanni</u>	Middle Volgian	▼
<u>N. (L.) duboisiana</u>	Middle Volgian	▲
<u>N. (L.) asiatica</u>	Middle Volgian	◆
"	Upper Volgian	■
<u>N. (L.) groenlandica</u>	Ryazanian	⊠
<u>N. (L.) laevis</u>	Ryazanian	○
"	Valanginian	●

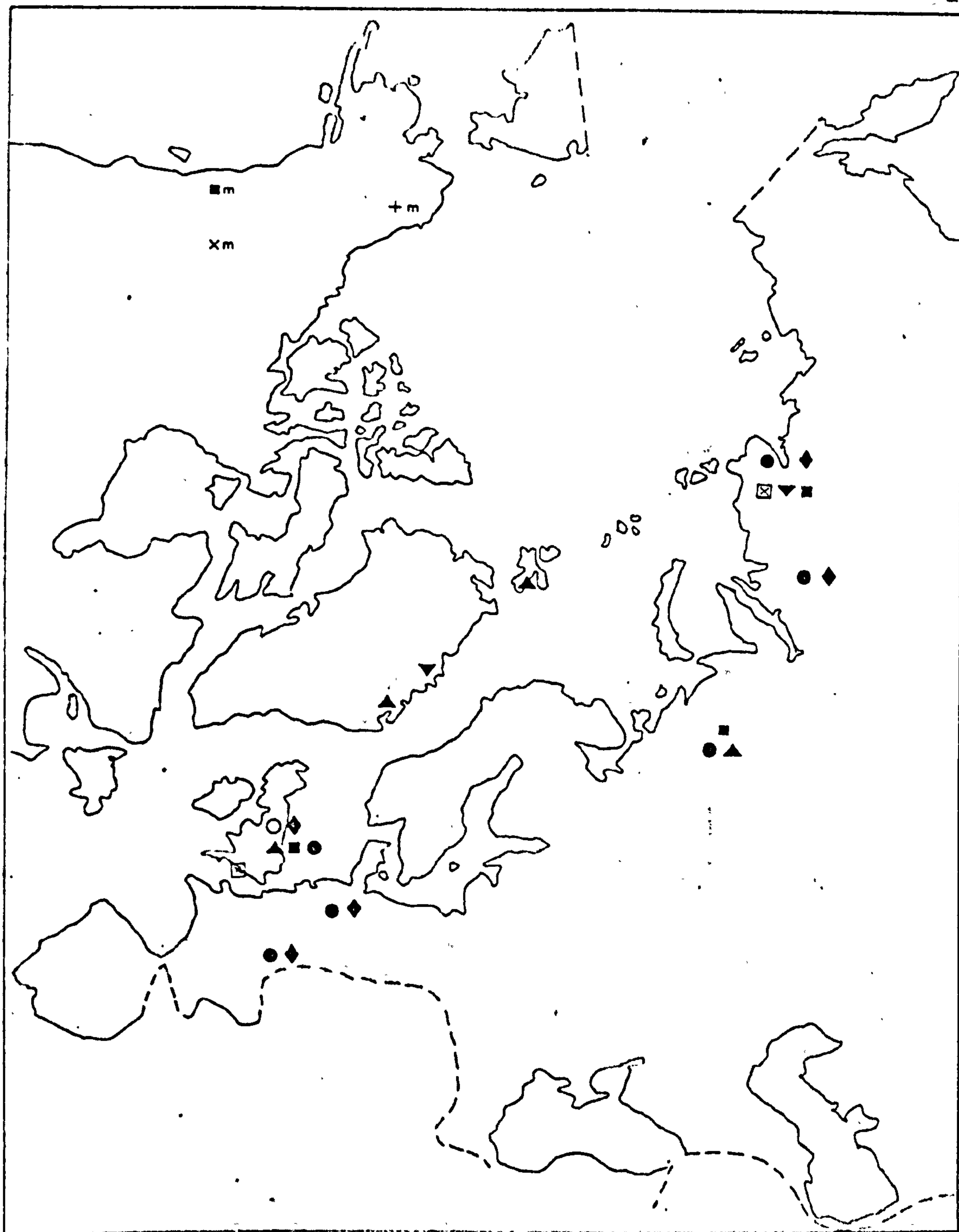


Figure 5.5

Distribution of Camptonectes (Rorcionectes) including Mclearnia which are distinguished by the symbol: m.

+ Albian
x Aptian
O Barremian

♦ Hauterivian
● Valanginian
■ Ryazanian

▲ Volgian
▼ Kimmeridgian
☒ Oxfordian

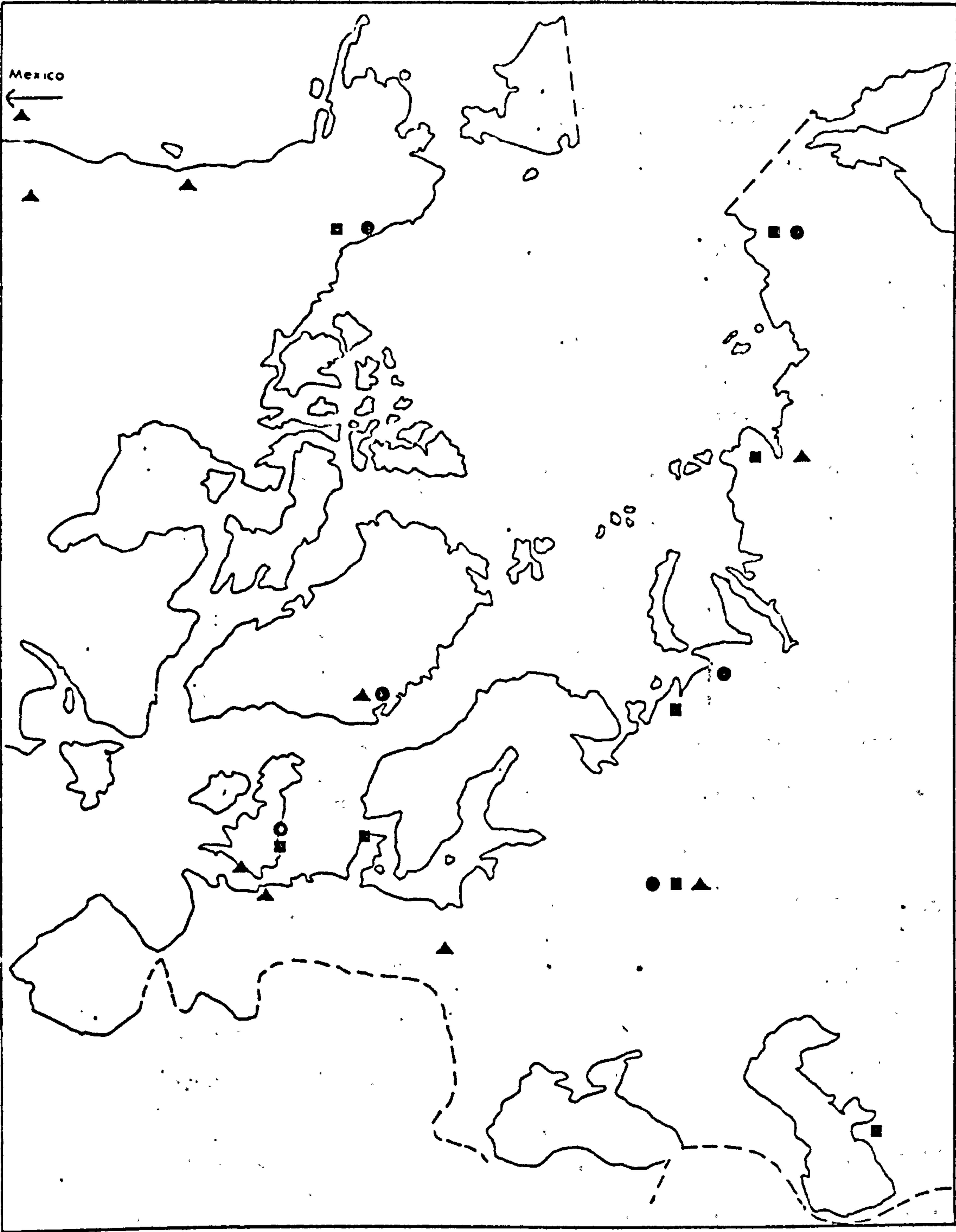


Figure 5.6

Geographic distribution of Spilsby Buchia.

<u>Buchia rugosa</u> s. s.	Middle Volgian	●
<u>Buchia mosouensis</u> assemblage	Middle Volgian	▲
<u>Buchia volgensis</u>	Ryazanian	■

within most of the Boreal Realm include Buchia and Camptonectes (Boreionectes). Buchia ranges beyond into Tethyan regions.

The principal factors controlling the distribution of the 'Spilsby' fauna are the distribution of suitable shallow marine facies and land masses. With changing sealevels the palaeogeography changes. The distribution of the land masses of the Boreal Realm are shown in figures 5.6 - 5.8, reconstructed for Middle Volgian, Upper Volgian and Ryazanian times respectively. The present day land masses are shown returned to their pre-drift positions after Smith, Briden and Drewry (1973). The North Pole is located in Alaska at 100 my (Smith et al. 1973) and just off the north of Alaska at 130 my by Van der Voo and French (1974). There are still arguments regarding the exact position of Greenland relative to Scandinavia which cannot be discussed here. Spain is shown in the rotated position and far eastern Siberia is restored to its position off Alaska (as shown by Rawson, 1973). Southern Europe is not illustrated. The palaeogeographic reconstructions are based on the works of Casey (1971, 1973), Enay (1972), Jelletzky (1971), Kringolts and Louppov (1975) and Saks (Ed. 1972).

In Middle Volgian times (fig. 5.6) there was probable open marine sea ways from eastern England south westwards and certainly to the east via the Danish Polish furrow and to the north east past East Greenland and Norway. At this time endemism on the East Midlands Shelf was relatively low, but was high in the partially enclosed Anglo-Paris basin. By Upper Volgian times, the marine south western approaches to the East Midlands shelf were uplifted and the Danish-Polish furrow was probably also sealed. Definite marine access only remained to the northwest. Endemism on the

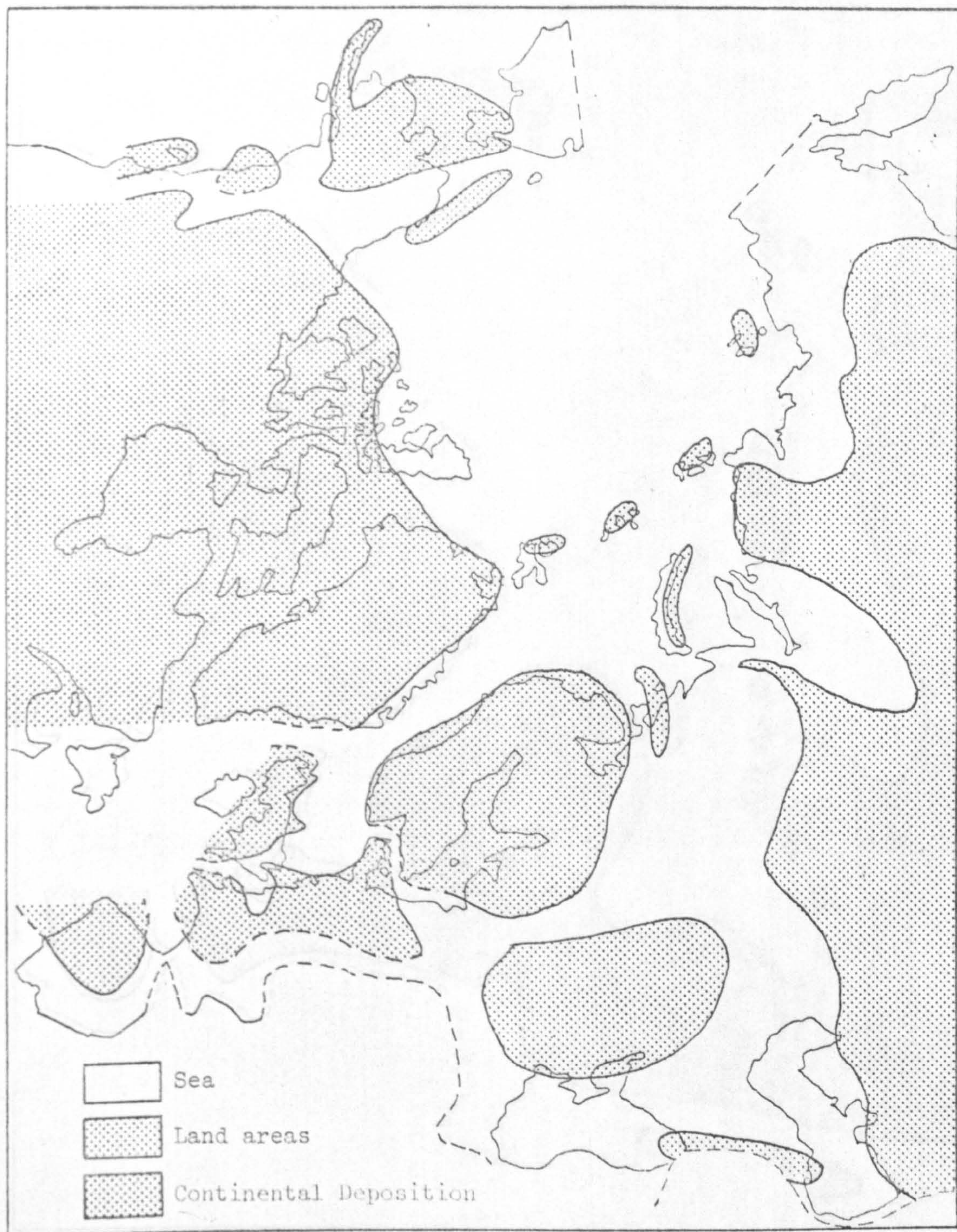


Figure 5.7

Reconstruction of the Boreal Realm in the Middle Volgian, showing the distribution of land and sea. Based on Jeletzky (1972), Enay (1972) Saks Ed. (1972) and author's observations.



Figure 5.8

Reconstruction of the Boreal Realm in the Upper Volgian, showing distribution of land and sea. See figure 5.7 for key. Based on Enay (1972), Saks (1972), Jeletzky (1973), Krimholtz and Louppov (1975) and author's observations.

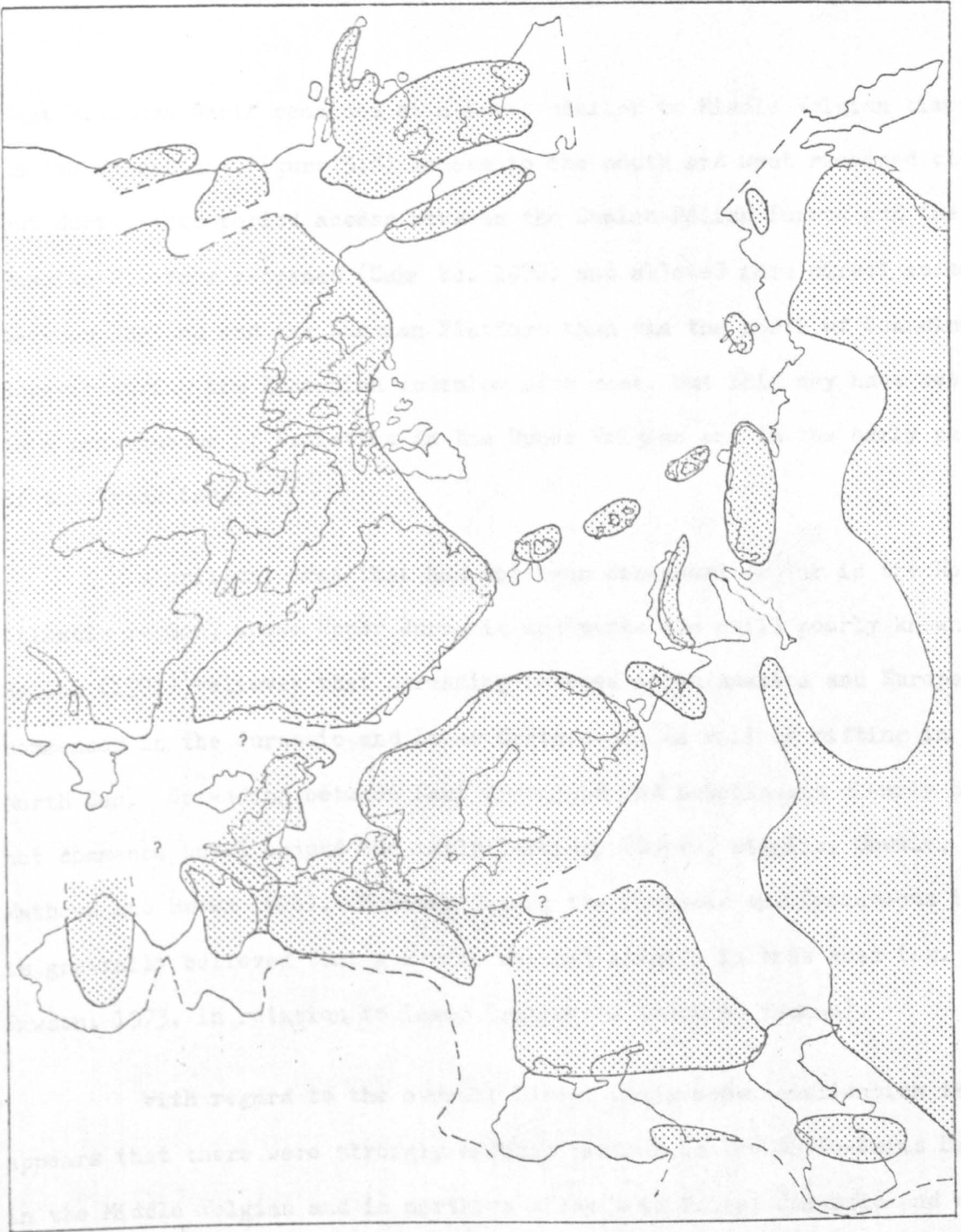


Figure 5.9

Reconstruction of the Boreal Realm in the Ryazanian, showing the distribution of land and sea. See Figure 5.7 for key. Based on Saks Ed. (1972), Casey (1973), Krimholtz and Louppov (1975), Jeletzky (1973) and author's observations.

East Midlands Shelf remained at a level similar to Middle Volgian times. In the Ryazanian (Figure 5.8) access to the south and west remained closed, but during this period access between the Danish-Polish Furrow and the Russian Platform reopened (Saks Ed. 1972) and allowed more direct access between England and the Russian Platform than via the north of Scandinavia. However during the Ryazanian endemism also rose, but this may have been as a consequence of isolation in the Upper Volgian and in the early part of the Ryazanian.

A critical area that has not been discussed so far is the North Atlantic region, whose Upper Jurassic sediments are still poorly known. Hallam (1971) believes that spreading between north America and Europe commenced in the Jurassic and Lower Cretaceous, as well as rifting in the North Sea. Spreading between East Greenland and Scandinavia clearly did not commence until around the early Tertiary (Soper, Higgins, Downie, Mathews and Brown 1976). However during the Jurassic and Cretaceous it is generally believed that a marine channel existed in this area (eg. Rawson, 1973, in relation to Lower Cretaceous ammonite faunas).

With regard to the overall Boreal Realm provincialisation it appears that there were strongly endemic centres in the Anglo-Paris Basin in the Middle Volgian and in northern Siberia in latest Jurassic and early Cretaceous times. A North European province stretches from England and East Greenland to the Russian Platform. A Siberian province exists in Russia east of the Urals. East Greenland and the North Urals act as transition zones between the provinces.

Chapter 6. CONCLUSIONS.

1. Ninety two species of bivalves have been recognised from the Spilsby Sandstone and contiguous strata. Of these forty five are described including the following new species:

Grammatodon (G.) spilsbiensis

Cucullaea (Dicranodonta) benniworthensis

Musculus (M.) derehamensis

Iotrigonia atlantica

Myophorella (M.) claxbiensis

Discoloripes septentrionalis

Neocrassina (Lyapinella) groenlandica

Neocrassina (Pressastarte) woldsi

Anisocardia (Antiquicyprina) lincolnshirensis

Anisocardia (Antiquicyprina) sandringhamensis

Hartwellia (Hartwellia) mintlyni

Girardotia wrighti

Goniomya (Goniomya) rawsoni

and the new subgenus Hartwellia (Claxbya).

2. The almost exclusive preservation of the fauna in calcareous, sideritic and phosphatised concretions in otherwise barren poorly cemented sediments suggests that the fauna was originally more widespread in the sediment but has been selectively preserved by early postdepositional diagenesis.

3. Although many of the bivalve species are long lived, the more rapidly evolving species are good for stage and substage correlation in parts of the Boreal Realm (see figure 3.1).

4. Five bivalve dominated assemblages are recognised, occurring in shallow marine facies of sands and silts and conglomerates including condensed horizons. The nature of the substrate controls the composition of the assemblages. The spacial distribution of the assemblages together with other information is used to construct tentative palaeogeographic reconstructions of southern and eastern England (see figures 4.23-26).

5. Jurassic bivalve diversity in Western Europe reaches a peak in the Volgian. In the Ryazanian it drops considerably because of widespread regression at this time, though in eastern England the reduction from Middle Volgian to late Ryazanian times is moderately gradual.

6. The bivalve fauna of the Middle Volgian to Ryazanian of eastern England does not compare well with that of the contemporary calcareous-dominated facies of the Portland and Purbeck Beds of southern England, although it does compare well with the partially contemporary arenaceous facies of the Upper Kimmeridgian. Geographically the fauna shows a very high degree of correlation with those of East Greenland and the Russian Platform, indicating a strong Boreal Influence.

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Appendix 1.

Section details with faunal lists.

This section provides where possible, bed by bed descriptions of the localities in the Spilsby Sandstone that have been examined during the course of this study. Faunal lists accompany each section. In addition to these localities, there are further collections in the IGS made by Dr. R. Casey, principally from the Sandringham Sands of Norfolk from localities that are no longer open. The stratigraphic information has been published elsewhere, eg. Casey and Gallois (1973), but faunal lists are given here according to the published bed numbers where possible. The number after the taxon gives the number of specimens seen in collections from each horizon and is an indication of the relative abundance of the fauna.

In the Nettleton area, a number of localities have been examined and the beds can be traced from one locality to the next. Consequently a single bed numbering system is used for localities 2-6 inclusive and the combined faunal list is given after locality 6.

The in situ localities are dealt with first, starting from the north and working southward, followed by the localities from which erratic material has been recovered.

Locality 1. Speeton foreshore, Yorkshire. See Neale 1962 for section.(SRAK).

Bed D6A

Nanogyra sp.

?Martesiid borings in wood (Neale 1968)

Bed D6D

Stegoconcha sp.

Bed D6H

Oxytoma sp.

Limea bodylevskii

Bed E

Grammatodon schourovskii

Licstrea plastica

Discoloripes cf. inequalis

Gastrochaena type borings in phosphatic nodule

Bed D6 unspecified level (Neale 1968)

Dicranodonta vagans

Pinna sp.

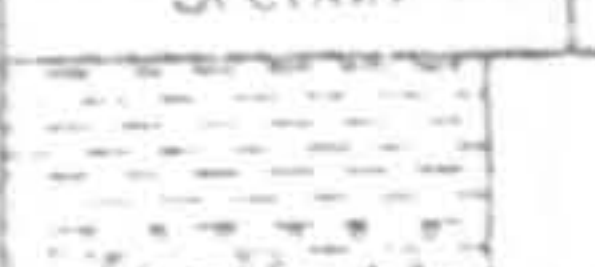

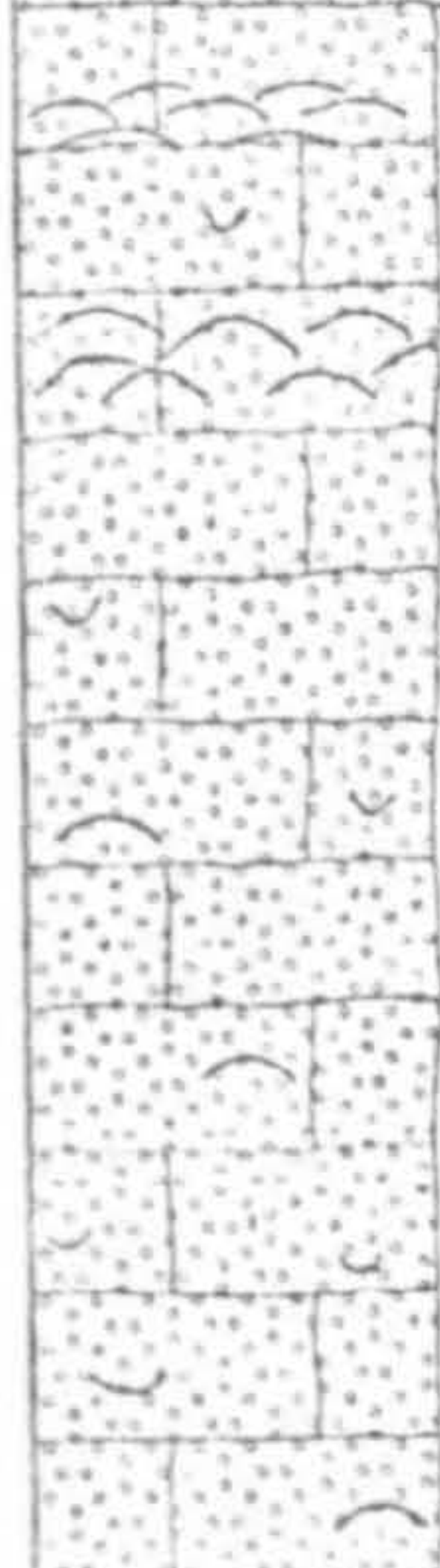
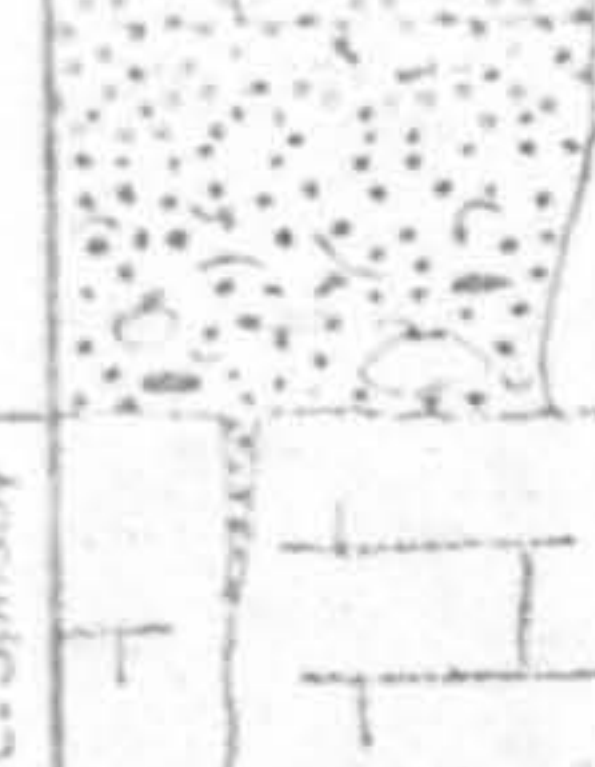
Oxytoma sp.

Lucinid


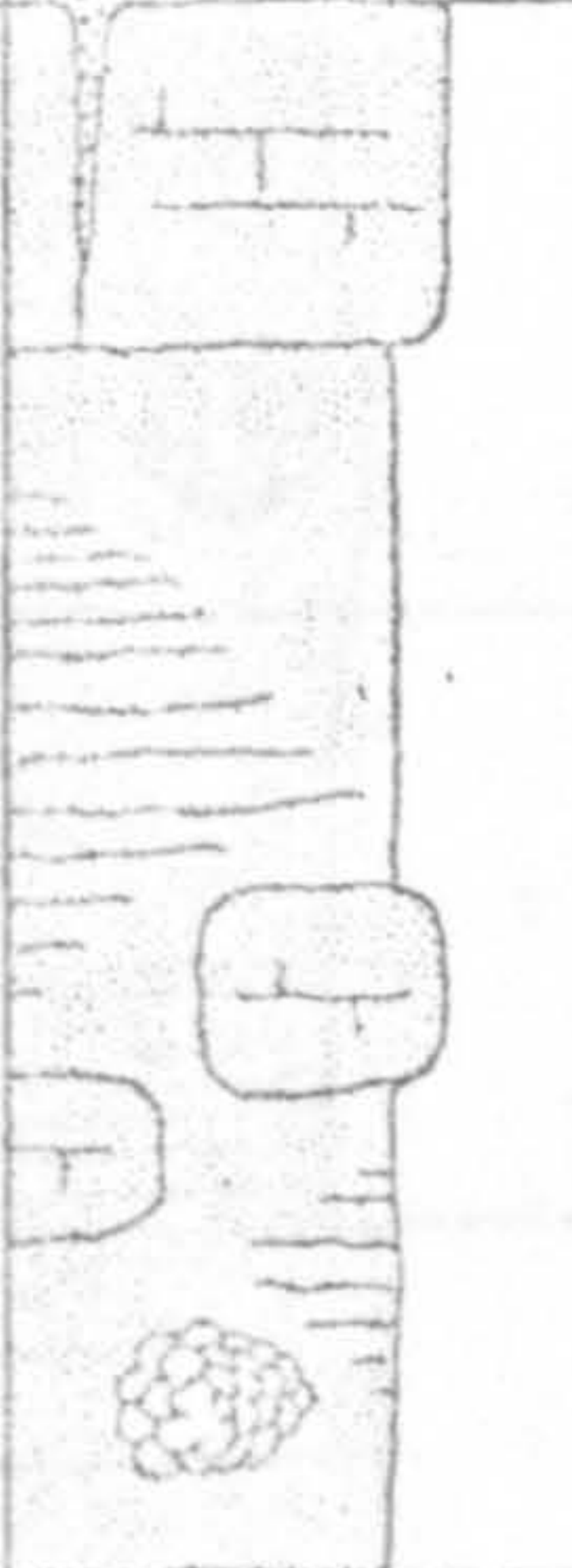
Astartid

Thracia sp.

Locality 2. Trial trench on Nettleton Hill, 500m north of Top Barn,
Nettleton, Lincs. TF 107994. Section measured October 1972.



Fm	Section	Bed	Thickness	Description
Tealby Fm.		14	0.30m+	Brown silty clay with scattered limonite oolites in basal 0.8m.
Claxby Formation		13	1.60	Red brown weathered limonite oolite with irregular 0.02m thick calcareous concretions which are relatively free from oolites. Lower 0.5m is more clayey but with oval calcareous concretions 0.1m in diameter. Scattered <u>Aetostreon</u> near top of bed.
		12	0.30	Densely oolitic unconsolidated limonite oolite with abundant <u>Entolium</u> , <u>Boreionectes</u> and brachiopods.
		11	0.35	Heavily ironstained limonite oolite with thin clay and limonite seams.
		10	0.10	Conglomerate of heavily limonitised <u>Acroteuthis</u> and <u>Lydites</u> .
		9	0.35	Massive earthy limonite oolite with thin fibrous calcite seam at base.
		8	3.00	Massive blocky weathering limonite oolite with two layers of <u>Boreionectes</u> in current stable position near top. Scattered <u>Aetostreon</u> , <u>Boreionectes</u> and <u>Plagiostoma</u> throughout the bed. Base gradational.
L. Spilsby		7	0.30	Lyditic conglomerate in pale buff marl, locally concretinised. Rich fauna of bivalves and gastropods. Some phosphatised pebbles and lumps of sandstone as in top of bed 6. Sharp base but irregular often filling fissures in bed below.
		6	0.50	Indurated medium to coarse grained calcite cemented sandstone.

Locality 3. Nettleton Hill Sand Pit, 400m north of Top Barn, Nettleton, Lincs. TF 107994-109994. Pit opened in 1971 and is expanding northwards.

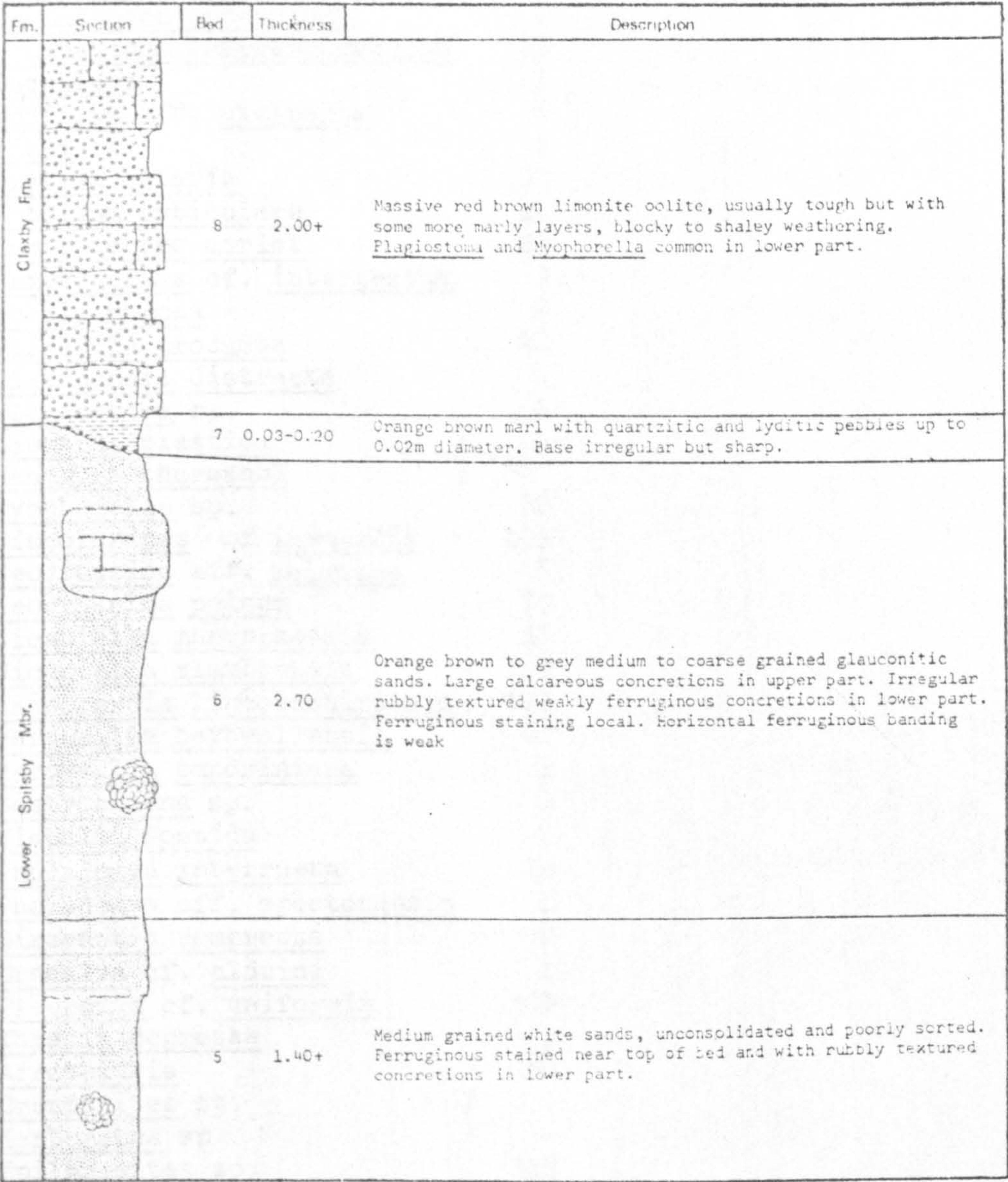
Fm.	Section	Bed	Thickness	Description
Claxby Fm.		8	3.00m+	Massive limonite oolite. Dark brown with common <u>Plagiostoma</u> , <u>Camptonectes</u> , <u>Aetostreon</u> and <u>Acroteuthis</u> . Limonitised lydite pebbles in lowest 0.10m. Base transitional.
		7	0.30	Lydite conglomerate in dark brown marl at east and west ends of section, but in between locally paler and more calcareous with abundant fossils and phosphatised lumps of Spilsby Sandstone from bed 6. Sometimes fills fissures in sandstone below.
Lower Spilsby Mbr.		6	3.00	Poorly sorted medium to coarse grained unconsolidated pale brown glauconitic sands. At top is 0.50m thick indurated calcite cemented sandstone with <u>Entolium</u> and <u>Myophorella</u> . Calcareous concretions in middle of bed contain rich fauna of molluscs including <u>S. lamplughii</u> . Horizontal ferruginous banding occurs and locally there are weakly ferruginised masses of rubbly textured concretions.
		5	2.00+	Poorly sorted white glauconitic sands locally ironstained but with irregular c0.08m flattened ferruginous concretions.

Locality 4 Hill slope 100m north east of Top Barn, Nettleton Lincs.
TF 108990. Abundant loose material from basal Spilsby nodule level, Bed 2.

Locality 5. Trial Sand Pit, 200m south east of Top Barn, Nettleton, Lincs.
TF 108989. Pit opened in early 1972 and has subsequently been bulldozed over. Phosphatised nodules from bed 2 can still be found.

Fm	Section	Bed	Thickness	Description
Lower Spilsby Mbr.		6	2.00+	Pale red brown medium grained sands. Poorly sorted and unbedded. Some horizontal Liesegang staining. Masses of weakly ferruginous c0.05m spherical concretions near base. Near the visible top large calcareous concretions 1m wide and 0.50 m thick. Rich molluscan fauna including <u>S. lamplughii</u> .
		5	1.00	Medium grained white sands, uncemented except for tabular ferruginous banding in the lower part.
		4	0.80	Ferruginous cemented medium to coarse grained sandstone. Red brown when weathered, but greenish when fresh. Fossiliferous in lower part with <u>S. primitivus</u> . At the base are 0.10m concretions of phosphorite.
		3	0.60	Poorly consolidated medium to fine grained glauconitic silty sands. Grey in upper part becoming ferruginous below with light coloured base. Partly phosphatised ammonite remains.
		2	0.20	Brown to blue silty to clayey glauconitic sands with common heavily phosphatised and bored concretions and fossils.
Kimmeridge Fm.		1	1.00+	Plastic blue grey clays with cementstone concretions up to 0.20m thick. Top surface burrowed into from bed 2, but sharp.

Locality 6. Sand Pit 700m north of Nettleton Top Farm, including trackside cutting leading to it from the south, Nettleton, Lincs. TF 116988-115984. The pit was last worked in 1971, but was bulldozed over and grassed the following year. The Claxby/Spilsby junction can still be seen in the trackway.



Localities 2-6, combined faunal list (SRAK)

Bed 2. Preservation as moulds in moderately to strongly phosphatised nodules.

<u>Bryozoan</u>	1
<u>Lingula</u>	1
<u>Rhynchonella aff. subvariabilis</u>	21
<u>Rouillieria ovoides</u>	28
<u>Bathrotomaria</u>	31
<u>Naticid</u>	3
<u>Gastropod indet</u>	38
<u>Barbatia cf. mysis</u>	33
<u>Grammatodon schourovskii</u>	198
<u>Grammatodon productum</u>	9
<u>Grammatodon compressiusculum</u>	33
<u>Cucullaea</u>	2
<u>Modiolus aff. vicinalis</u>	8
<u>Pinna sp</u>	6
<u>Oxytoma octavia</u>	23
<u>Entolium orbiculare</u>	21
<u>Camptonectes morini</u>	22
<u>Camptonectes cf. intertextus</u>	9
<u>Buchia rugosa</u>	2
<u>Plicatula producta</u>	42
<u>Placunopsis distracta</u>	1
<u>Plagiostoma sp.</u>	34
<u>Lioptrea plastica</u>) 137
<u>Nanogyra thurmanni</u>	
<u>Myophorella sp.</u>	36
<u>Discoloripes cf. inequalis</u>	139
<u>Neocrassina aff. asiatica</u>	4
<u>Neocrassina pelops</u>	78
<u>Nicaniella mnevnikensis</u>	35
<u>Nicaniella claxbiensis</u>	3
<u>Anisocardia lincolnshirensis</u>	171
<u>Hartwellia hartwellensis</u>	42
<u>Hartwellia cancriniana</u>	1
<u>Gastrochaena sp.</u>	3
<u>Fiatella foetida</u>	47
<u>Pholadomya interrupta</u>	22
<u>Pholadomya aff. spectonensis</u>	1
<u>Girardotia compressa</u>	8
<u>Gresslya cf. alduini</u>	1
<u>Pleuromya cf. uniformis</u>	300
<u>Thracia depressa</u>	3
<u>Acroteuthis</u>	50
<u>Crendonites sp.</u>) 313
<u>Kerberites sp</u>	
<u>Epilaugeites sp.</u>	
<u>Lomonosovella sp.</u>	
<u>Pavlovia sp.</u>	
<u>Wood</u>	2
<u>Bone (Reptilian)</u>	1
<u>Gastrochaena</u> type borings in phosphatised nodules abundant	

Bed 4. Preservation as composite moulds or in weakly phosphatised nodules.

<u>Bathrotomaria</u> sp.	3
Gastropoda indet.	2
<u>Pinna</u> cf <u>constantini</u>	3
<u>Entolium orbiculare</u>	12
<u>Camptonectes morini</u>	1
<u>Plagiostoma subrigida</u>	3
<u>Myophorella intermedia</u>	15
<u>Discoloripes</u> cf. <u>inequalis</u>	90
<u>Neocrassina asiatica</u>	3
<u>Neocrassina woldsi</u>	5
<u>Hartwellia</u> sp.	70
<u>Pleuromya</u> cf. <u>uniformis</u>	7
<u>Acroteuthis</u> sp	5
<u>Subcraspedites primitivus</u> group	63

Bed 6. Preservation principally as moulds in calcareous concretions.

Gastropod indet	1
<u>Pinna</u> cf. <u>subcuneata</u>	5
<u>Anopaea sphenoides</u>	4
<u>Oxytoma octavia</u>	2
<u>Entolium orbiculare</u>	134
Ostreid	2
<u>Myophorella intermedia</u>	6
<u>Discoloripes fischerianus</u>	6
<u>Neocrassina asiatica</u>	18
<u>Neocrassina woldsi</u>	3
<u>Pholadomya interrupta</u>	3
<u>Pleuromya uniformis</u>	3
<u>Acroteuthis</u> sp.	15
<u>Subcraspedites lamplughii</u>	20
Plesiosaurian vertebra	1

Locality 7. Sand pit 800m north west of Donnington on Bain Church, Lincs.

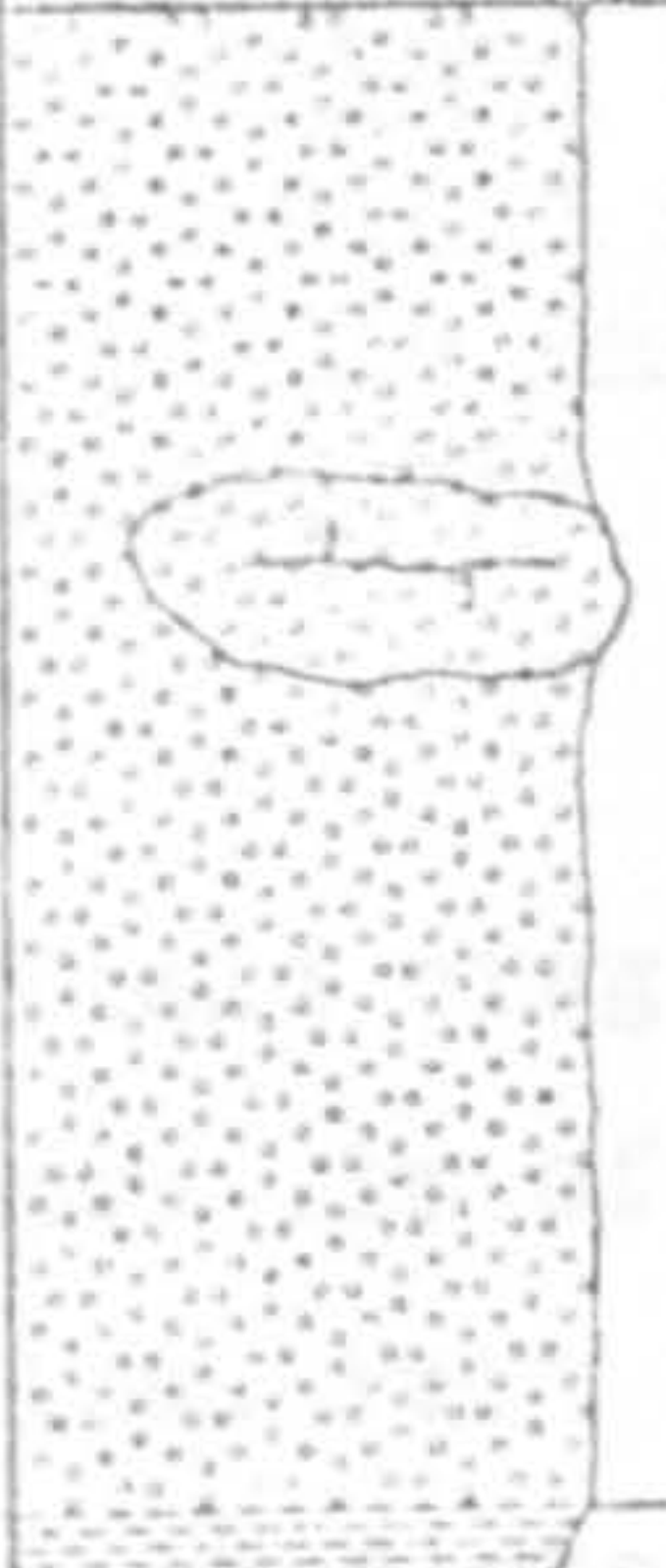
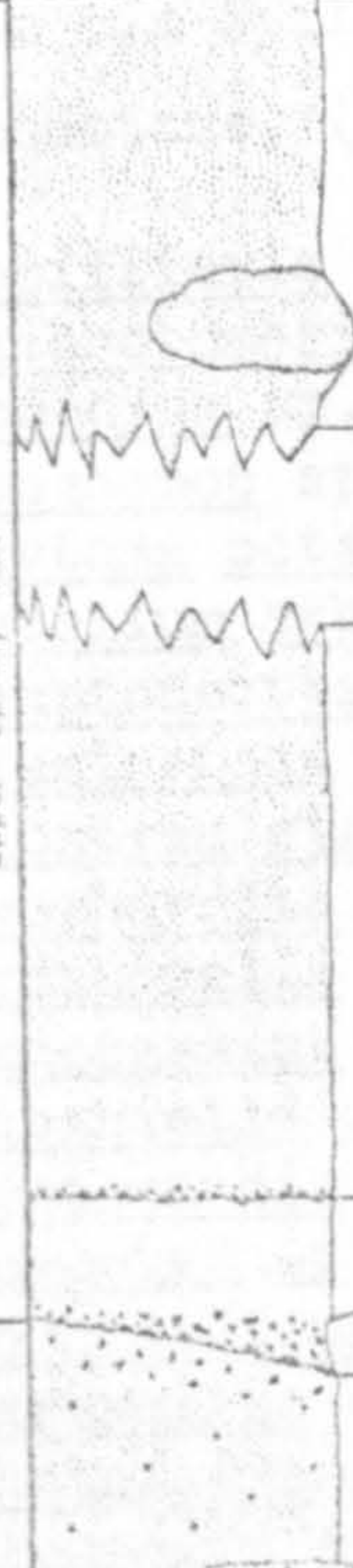

TF 233837. Although disused and partially flooded, about 2m of haematite stained sandstone (Ferruginous Grit?) yealds common moulds of Entolium orbiculare (SRAK).

Locality 8. Biscathorpe Wold Gravel Pit, Lincs. TF 2184. (Thurrel 1957).

Clayey coarse glauconitic sands with rich fauna of brachiopods, gastropods, bivalves and belemnites. Casey (1973) has identified the age as Upper Ryazanian, P. albidum Zone. The bivalve fauna is not described in the text, but is listed here. Calcitic shell is preserved. (IGS)

<u>Nucula</u> sp.	2
<u>Barbatia</u> sp.	4
<u>Dicranodonta benniworthensis</u>	92
<u>Musculus</u> sp.	2
<u>Entolium orbiculare</u>	6
<u>Boreionectes cinctus</u>	2
<u>Nanogyra thurmanni</u>	4
<u>Myophorella claxbiensis</u>	25
Lucinid	4
<u>Neocrassina laevis</u>	25
<u>Pressastarte woldsi</u>	2
<u>Nicaniella claxbiensis</u>	15
<u>Protocardia</u> sp.	15
<u>Corbicellopsis claxbiensis</u>	68
<u>Tancredia</u> sp.	1
<u>Procyprina centralis</u>	94
<u>Pleuromya uniformis</u>	6

Localities 9/10. Locality 7, upper part of section: disused railway cutting at Benniworth Haven, 1km south west of Donnington on Bain, Lines. TF 227824. Locality 8, lower part of section: railway cutting 0.7km south of Donnington on Bain. TF 234823.

Em.	Section	Bed	Thickness	Description
Clayey Fm.		9	2.00m+	Red brown limonite oolite marl with calcareous concretions approximately 1-2m above base. Concretions are richly fossiliferous with <u>Myophorella</u> , <u>Cucullaea</u> , <u>Plagiostoma</u> , <u>Camptonectes</u> etc. also with ' <u>Proleopoldia</u> '. Base gradational.
		8	0.30	Grey plastic oolite free clay, weathers brown.
Upper Spilshy Mbr.		7	7.50+	Pale medium grained glauconitic sands, locally cemented.
				Unmeasured break or overlap.
		6	3.00+	Pale brown medium to fine grained sands without lyditic pebbles except in thin seam at base. Generally structureless except for clay seam 2m above base.
		5	0.30	Medium to fine grained pale ferruginous sands.
		4	0.05-0.20	Lyditic conglomerate with belemnite moulds, partly phosphatised, in medium grained sand.
Lower Spilshy Mbr.		3	0.50-0.65	Massive medium to coarse grained ferruginous sands with lyditic pebbles. Base locally with calcareous cement.
		2	0.60	Relatively unferruginised medium to coarse grained sandstone with isolated valves of <u>Entolium</u> .
		1	1.30+	Medium to coarse grained sands. Heavily ferruginised with Liesegang banding in the upper part. Greenish brown in lower part. Abundant moulds of <u>Entolium</u> and some small calcareous concretions.

Locality 11. Roadside pit, 100m north west of Moses Farm, Stenigot, Lincs.

TF 248812. 2m of ferruginous sands visible of Upper Spilsby Sandstone. The following fauna was collected as moulds from loose blocks (SRAK).

<u>Terebratulid</u>	1
<u>Boreionectes cinctus</u>	5
<u>Plagiostoma</u> sp.	5
<u>Neocrassina asiatica</u>	3
<u>Pleuromya uniformis</u>	1
<u>Surites</u> sp.	1



Locality 12. Field crag 100m east of Winceby Rectory, Lincs. TF 320685

Shows .1m of phosphatised conglomerate channeled into sands below. From the conglomerate comes indigenous Surites sp. and reworked phosphatised Subcraspedites lamplughii which represents the mid Spilsby nodule bed at the base of the Upper Spilsby Sandstone. (IGS & SRAK).

<u>Rouillieria</u> sp.	1
<u>Bathrotomaria</u> sp	4
<u>Modiolus</u> sp.	1
<u>Isognomon</u> sp	1
<u>Oxytoma octavia</u>	1
<u>Entolium orbiculare</u>	14
<u>Camptonectes morini</u> (unphosphatised)	2
<u>Plagiostoma subrigida</u>	1
? <u>Liostrea gigantea</u>	3
<u>Myonhorella intermedia</u>	8
<u>Myonhorella keepingi</u> (unphosphatised)	1
<u>Neocrassina asiatica</u>	5
<u>Nicaniella claxbiensis</u>	1
<u>Protocardia concinna</u>	1
<u>Sowerbya longior</u>	1
<u>Corbicellopsis claxbiensis</u>	1
<u>Hartwellia</u> sp.	1
<u>Pholadomya</u> sp.	1
<u>Pleuromya</u> sp.	3
<u>Acreteuthis</u> sp.	2
<u>Armonites</u>	2+

Locality 13. Field crag 600m south of Highfield Farm, Winceby, Lincs.

TF 325692. (SRAK)

Fm.	Section	Bed	Thickness	Description
Upper Spilsby Mbr.		4	0.60	Pale red brown unconsolidated medium to fine grained glauconitic sand. At base lyditic conglomerate up to 0.20m thick with scattered phosphatised lumps of sandstone.
		3	0.50	Moderately consolidated medium grained red brown glauconitic sands. At base 0.10m lydite conglomerate with phosphatised lumps of sandstone.
		2	0.50	Red brown moderately consolidated medium to coarse grained glauconitic sands. At base 0.10m conglomerate of lydites and lumps of phosphatised sandstone with abundant fossils in poor preservation..
Lower Spilsby Mbr.		1	4.00+	Pale reddish medium to coarse grained sands with sparse lydites. Locally well consolidated.

Bed 2. Preservation as phosphatised moulds.

<u>Entolium orbiculare</u>	2
<u>Myophorella intermedia</u>	2
? <u>Liostrea gigantea</u>	1
<u>Protocardia concinna</u>	1
<u>Sowerbya longior</u>	4

Locality 14. Field crag 300m south east of Ramshaw Farm, Winceby, Lincs.


TF 331688. About .3m of phosphatised lumps of sandstone and fossils are visible. Loose blocks excavated from ditches immediately below yielded Surites sp. indicating probably the mid Spilsby Sandstone. The following fauna is preserved as moulds (SRAK).

In situ:	<u>Entolium orbiculare</u>	2
	<u>Boreionectes cinctus</u> :	1
	<u>Plagiostoma subrigida</u>	4
	? <u>Liostrea gigantea</u>	1
	<u>Myophorella intermedia</u>	3
	<u>Neocrassina asiatica</u>	4
	<u>Protocardia concinna</u>	1
	<u>Pholadomya</u> sp.	1
	<u>Acroteuthis</u> sp	3
	Ammonites	4
	Wood	1

From loose blocks below:

Gastropod indet.	1
<u>Cucullaea vagans</u>	1
<u>Mulletia</u> sp.	3
<u>Sowerbya longior</u>	1
Bone fragment	2

Locality 15. Disused sand pit and adjacent road cutting, 600m west of Harrington Hall, Lincs. TF 361719.

Fm	Section	Bed	Thickness	Description
Lower Spilsby Fm.		6	0.20m+	Flaggy red brown medium grained sandstone.
		5	0.15	Hydrite and belemnite conglomerate in medium grained sandstone.
		4	0.25	Two layers of flaggy red brown medium grained sandstone.
		3	1.00	Green brown medium to coarse grained sands, soft when fresh, hard when weathered. Lenticular structures when weathered. Base gradational.
		2	0.50	Soft easily eroded medium to coarse grained sands. Moulds of <i>Entolium</i> and belemnites. Locally brown mottled to black. Scattered large calcareous concretions with rich molluscan fauna of bivalves and <i>S. sowerbyi</i> . Base gradational.
		1	1.30	Massive red green coarse grained sands with some coarse Liesegang staining.

Bed 2. Preservation principally as moulds in calcareous concretions (SRAK).

<u>Patellid</u>	1
<u>Musculus fischerianus</u>	1
<u>Anopaea sphenoidea</u>	1
<u>Entolium orbiculare</u>	98
<u>Discoloripes fischerianus</u>	2
<u>Neocrassina asiatica</u>	2
<u>Neocrassina woldsi</u>	2
<u>Protocardia concinna</u>	1
<u>Sowerbya longior</u>	14
<u>Corbicellopsis claxbiensis</u>	1
<u>Procyprina centralis</u>	3
<u>Acroteuthis sp.</u>	1
<u>Subcraspedites sowerbyi group</u>	5

Locality 16. Disused sand pit at High Barn, 1km north west of West Keal, Lincs. TF 362643. Lower part of section visible in April 1974 has been subsequently destroyed. (SRAK).

Fm	Section	Bed	Thickness	Description
Upper Spilsby Fm.		5	1.00+	Medium grained glauconitic sands, weathering green brown. Occasional coarser clasts up to 5mm.
		4	0.10	Belemnite conglomerate preserved as moulds with occasional phosphatised lumps of sandstone.
		3	1.00	Green brown weathering medium grained sands.
Lower Spilsby Fm.		Unmeasured gap.		
		2	1.40+	Pale medium to coarse grained sands with calcareous concretions 1m above base. No fauna recorded.
		1	0.70+	Pale medium to coarse grained sands with 0.5m thick tough calcite cemented concretionary layer at top. <u>S. sowertyi</u> and rich bivalve fauna.

Bed 1. Preservation principally as moulds in calcareous concretions

<u>Patellid</u>	2
<u>Gastropod indet.</u>	13
<u>Lucullaea vagans</u>	10
<u>Musculus fischerianus</u>	2
<u>Modiolus cf. sibiricus</u>	1
<u>Falcimytillus suprajurensis</u>	1
<u>Pinna aff. subcuneata</u>	14
<u>Anopaea sphenoidea</u>	2
<u>Entolium orbiculare</u>	674
<u>Camptonectes morini</u>	4
<u>Pseudolimea arctica</u>	1
<u>Nanogyra thurmanni</u>	1
<u>Myophorella intermedia</u>	7
<u>Myophorella tealbyensis</u>	35

<u>Discoloripes fischerianus</u>	35
<u>Neocrassina asiatica</u>	48
<u>Pressastarte woldsi</u>	11
<u>Nicaniella</u> sp.	1
<u>Trautscholdia claxbiensis</u>	6
<u>Protocardia concinna</u>	15
<u>Sowerbya longior</u>	62
<u>Corbicella claxbiensis</u>	1
<u>Procyprina centralis</u>	60
<u>Pholadomya interrupta</u>	1
<u>Goniomya</u> cf. <u>rawsoni</u>	1
<u>Pleuromya orbignyana</u>	43

Locality 17. Road Cutting 1km north of Spilsby, Lincolnshire. TF 399672

Loose block of medium grained glauconitic sandstone with
Subcraspedites sowerbyi, Lower Spilsby Sandstone, S.
preplicomphalus Zone, Upper Volgian (SRAK).

Gastropod	2
<u>Grammatodon spilsbiensis</u>	1
<u>Cucullaea vagans</u>	8
<u>Anopaea sphenoidea</u>	1
<u>Oxytoma octavia</u>	6
<u>Entolium orbiculare</u>	120
<u>Camptonectes morini</u>	2
<u>Myonhorella</u> sp.	7
<u>Discoloripes fischerianus</u>	11
<u>Neocrassina asiatica</u>	11
<u>Neocrassina woldsi</u>	4
<u>Trautscholdia claxbiensis</u>	2
<u>Sowerbya longior</u>	6
<u>Procyprina centralis</u>	5
<u>Corbula</u> sp.	14
<u>Acroteuthis</u> sp.	1
<u>Subcraspedites sowerbyi</u>	9
Echinoid spine	1

Locality 19. Pylon site, 650yds north 30° west of Church Farm, Bawsey, Norfolk. TF 65972080. Upper part of Mintlyn Beds, S. stenomphalus Zone, Ryazanian. Local shell accumulations in ferruginous medium to fine grained sandstone. (IGS)

<u>Camptonectes morini</u>	2
<u>Camptonectes cinctus</u>	2
<u>Myophorella keepingi</u>	1
<u>Neocrassina asiatica</u>	25
<u>Protocardia</u> sp.	30
<u>Corbicella claxbiensis</u>	3
<u>Corbula</u> sp.	85
<u>Pleuromya uniformis</u>	2
<u>Thracia phillipsi</u>	1
<u>Surites</u>	25

Locality 20. North Runcton. Casey and Gallois, 1973, p. 8. (IGS)

Bed 4. Runcton Beds reworked into highly phosphatised conglomerate.

<u>Myophorella intermedia</u>	2
<u>Neocrassina asiatica</u>	5
<u>Pressastarte</u> sp	1
<u>Nicaniella claxbiensis</u>	1
<u>Protocardia concinna</u>	11
<u>Hartwellia</u> sp.	1
<u>Pleuromya</u> sp.	3
<u>Subcraspedites</u> spp.	36

Bed 6. Basal Mintlyn Beds. Dark phosphatised moulds in dark green glauconitic sand.

Serpulid	1
Gastropod indet.	5
<u>Cucullaea vagans</u>	8
<u>Entolium orbiculare</u>	12
<u>Camptonectes morini</u>	2
<u>Myophorella keepingi</u>	15
<u>Neocrassina asiatica</u>	10
<u>Protocardia concinna</u>	64
<u>Sowerbya longior</u>	2
<u>Corbicella claxbiensis</u>	1
<u>Hartwellia</u> sp.	1
<u>Pleuromya uniformis</u>	7
<u>Thracia depressa</u>	1
<u>Acroteuthis</u> sp.	4
Ammonites	44

Bed 11. Mintlyn Beds. S. stenomphalus Zone, Ryazanian.

<u>Pleuromya uniformis</u>	1
<u>Surites</u> sp.	9

Bed 12. Mintlyn Beds, S. stenomphalus Zone, Ryazanian. Pale limonitic ironstone with moulds.

<u>Myophorella keepingi</u>	2
<u>Neocrassina groenlandica</u>	1
<u>Hartwellia ryazaniensis</u>	1
<u>Pleuromya</u> sp.	1
<u>Surites</u> sp.	35

Locality 21. Constitution Hill, West Winch. Casey and Gallois (1973, p. 8). Basal Cretaceous nodule bed. (IGS).

	In situ	Ex situ
<u>Terebratulid</u>	1	-
<u>Bathrotomaria</u>	8	-
<u>Neritopsis</u>	2	-
<u>Gastropoda</u> indet.	10	4
<u>Cucullaea vagans</u>	26	2
<u>Modiolus</u> sp.	1	-
<u>Entolium orbiculare</u>	2	1
<u>Camptonectes morini</u>	-	1
<u>Myophorella</u> sp.	-	6
<u>Neocrassina asiatica</u>	36	3
<u>Pressastarte woldsi</u>	2	-
<u>Protocardia concinna</u>	244	66
<u>Sowerbya longior</u>	4	2
<u>Corbicellopsis claxbiensis</u>	18	1
<u>Anisocardia sandringhamensis</u>	7	-
<u>Hartwellia</u> sp.	1	-
<u>Pleuromya</u> sp.	23	1
<u>Thracia</u> sp.	1	-
<u>Acroteuthis</u> sp.	6	1
<u>Subcraspedites</u> spp.	100	1

Locality 22. No 4 Gas Feeder Trench, 900yds north of West Winch Church, Norfolk. TF 631167. (IGS).

Ex situ material in preservation of grey, medium grained glauconitic sandstone. Roxham Beds, P. oppressus Zone, Middle Volgian.

<u>Rouillieria ovoides</u>	10
<u>Gastropod</u> indet.	1
<u>Modiolus</u> sp.	2
<u>Oxytoma octavia</u>	13
<u>Arctotis</u> cf. <u>intermedia</u>	1
<u>Entolium orbiculare</u>	18
<u>Camptonectes morini</u>	11
<u>Pseudolimea arctica</u>	22
<u>Ostreid</u>	4
<u>Myophorella</u> sp.	1
<u>Lucinid</u>	6
<u>Neocrassina asiatica</u>	2
<u>Pleuromya uniformis</u>	33
<u>Acroteuthis</u> sp.	1
<u>Paracraspedites</u> sp.	4

Ex situ material preserved as black phosphatised moulds. Remanie horizon of the Runcton Beds.

<u>Cucullaea vagans</u>	7
<u>Myophorella intermedia</u>	11
<u>Neocrassina asiatica</u>	8
<u>Protocardia concinna</u>	7
<u>Gastrochaena</u> sp.	2
<u>Pleuromya</u> sp.	2
<u>Subcraspedites</u> spp.	4

Locality 23. Drainage Channel, Wormgay, Norfolk. TF 656118. In preservation of basal Roxham Beds. (IGS)

<u>Entolium orbiculare</u>	1
<u>Myophorella</u> sp.	2
<u>Corbicella claxbiensis</u>	1
<u>Hartwellia</u> sp.	3
<u>Pleuromya</u> sp.	5

Locality 24. West Dereham Flood Relief Channel. Casey and Gallois, 1973.(IGS).

Beds 2-5 inclusive. Roxham Beds. Fossils preserved as pyritic skins.

<u>Cucullaea vagans</u>	4
<u>Myophorella</u> sp.	2
<u>Neocrassina</u> sp.	2
<u>Pleuromya</u> sp.	3
<u>Ammonites</u>	35

Bed 6. Reworked Runcton Beds. Fossils as black phosphatised moulds.

<u>Bathrotomaria</u> sp	3
<u>Gastropoda</u> indet.	6
<u>Cucullaea vagans</u>	120
<u>Isognomon</u> sp.	3
<u>Entolium orbiculare</u>	4
<u>Camptonectes morini</u>	2
<u>Myophorella intermedia</u>	30
<u>Discoloripes septentrionalis</u>	10
<u>Myoconcha</u> aff <u>portlandica</u>	1
<u>Neocrassina asiatica</u>	105
<u>Corbicellopsis claxbiensis</u>	30
<u>Anisocardia sandringhamensis</u>	30
<u>Hartwellia</u> sp.	30
<u>Martesia constricta</u>	6
<u>Pholadomya</u> sp.	3
<u>Subcraspedites</u> spp.	516
<u>Acroteuthis</u> sp.	21
Fish vertebrae	16
Fish teeth (crushing)	3
Reptilian vertebrae	15
Reptilian teeth	2
Large bone fragments	7
Wood fragments	14

Bed 7. Lower Mintlyn Beds. Fine sandy concretions with moulds of fossils.

<u>Entolium orbiculare</u>	190
<u>Nicaniella</u> sp.	50
Tellinid	1
<u>Anisocardia sandringhamensis</u>	68
<u>Hectoroceras</u> sp.	10
Fish vertebra	1

Bed 8. Lower Mintlyn Beds. Glauconitic sandy phosphatised moulds.

<u>Myophorella</u> sp.	2
<u>Neocrassina</u> sp.	2
<u>Hartwellia</u> sp.	1
<u>Hectoroceras</u> sp.	1

1-2' below C1 (IGS Catalogue). Grey concretions with much fine lignite
and drifted shelly material.

<u>Entolium orbiculare</u>	9
<u>Nicaniella</u> sp.	2
Tellinid	2

Band A. (IGS Catalogue). Green-purple clay ironstone with moulds.

<u>Neocrassina asiatica</u>	7
<u>Anisocardia sandringhamensis</u>	12
<u>Pholadomya mediana</u>	2
<u>Thracia phillipsi</u>	1
<u>Acroteuthis</u> sp.	2
<u>Hectoroceras</u> sp.	3
Crustacean	1
Wood Fragments	1

Bed C1 (IGS Catalogue). As Band A.

<u>Thracia phillipsi</u>	2
<u>Hectoroceras</u> sp.	20

Bed C2 (IGS Catalogue). Ferruginous weathering clay ironstone with moulds.

<u>Cucullaea vagans</u>	2
<u>Entolium orbiculare</u>	1
<u>Anopaea brachowi</u>	2
<u>Myophorella keepingi</u>	4
<u>Neocrassina groenlandica</u>	96
<u>Anisocardia sandringhamensis</u>	2
<u>Hartwellia mintlyni</u>	2
<u>Thracia phillipsi</u>	1
<u>Acroteuthis</u> sp.	1
<u>Hectoroceras</u> sp.	5
Wood with Martesiid borings	1

Beds 8-17 inclusive. Mintlyn Beds, H. kochi Zone, Ryazanian. Clay

Ironstone with fossils as moulds.

<u>Naticid</u>	1
<u>Gastropods indet.</u>	7
<u>Nuculoma varibilis</u>	4
<u>Cucullaea vagans</u>	6
<u>Anopaea brachowi</u>	2
<u>Oxytoma octavia</u>	1
<u>Entolium orbiculare</u>	22
<u>Camptonectes morini</u>	9
<u>Pseudolimea arctica</u>	1
<u>Iotrigonia atlantica</u>) 34
<u>Myophorella keepingi</u>	
<u>Neocrassina groenlandica</u>	587
<u>Pressastarte woldsi</u>	1
<u>Senis aff. petschorae</u>	2
<u>Sowerbya longior</u>	12
<u>Anisocardia sandringhamensis</u>	74
<u>Hartwellia mintlyni</u>	10
<u>Hartwellia cancriniana</u>	1
<u>Pholadomya mediana</u>	33
<u>Goniomya rawsoni</u>	4
<u>Girardotia wrighti</u>	1
<u>Pleuromya orbignyana</u>	29
<u>Thracia phillipsi</u>	14
<u>Acroteuthis sp.</u>	50
<u>Hectoroceras sp.</u>	40
<u>Crustacean</u>	1
<u>Fish vertebra</u>	1
<u>Wood fragments</u>	50

Bed 18. Base of Carstone. Reworked fossils phosphatised.

<u>Neocrassina sp.</u>	2
<u>Hectoroceras sp.</u>	present
<u>Craspedodiscus sp.</u>	present

Locality 25. Drainage ditch 275yds east of Snowre Hall, Fordon. TF 63089933.

Mentioned Casey and Gallois (1973, p. 6). (IGS).

Basal phosphatised nodule of the Roxham Beds.

<u>Neocrassina sp.</u>	1
<u>Lucinid</u>	2
<u>Anisocardia lincolnshirensis:</u>	1
<u>Pleuromya cf uniformis</u>	6
<u>Ammonites</u>	8

Basement Sands of the Roxham Beds.

<u>Pinna cf. constantini</u>	5
<u>Camptonectes morini</u>	17
<u>Anisocardia sandringhamensis</u>	1
<u>Pleuromya sp.</u>	1

Locality 26. British Industrial Sand Pit, Bawsey Warren (Leziate). Norfolk TF 672194. Erratic boulders of Lower Spilsby Sandstone from the drift occur around here, some may have been moved a short distance by earth moving equipment. The pit itself is worked in the upper part of the Mintlyn Beds and is probably of Valanginian age. The extensive collections from this locality (IGS & SRAK) are summarised in the table on the next page.

Locality 27. 6ft below surface opposite main shopin Southery, Suffolk. Soft brown medium grained glauconitic sandstone (NCM).

<u>Rouillieria ovoides</u>	2
<u>Neocrassina asiatica</u>	2

Locality 28. Soham Tracey Graveyard, Suffolk. Grey medium grained glauconitic sandstone. (NCM).

<u>Rouillieria ovoides</u>	13
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Locality 29. Reveningham. Grey glauconitic sandstone with lydites. (NCM).

<u>Rouillieria ovoides</u>	
<u>Neocrassina asiatica</u>	

Locality 30. Standing stone of grey medium grained glauconitic sandstone, roadside car park, 1.5km north west of Stockton, Norfolk. (SRAK)

<u>Rouillieria ovoides</u>	1
<u>Ophiomorpha</u> sp	several

Appendix 2.

Spilsby erratic block source information.

The following list gives the source of information concerning the distribution of erratic boulders of inferred Spilsby Sandstone origin which have already been shown on Figure 2.6 . For full bibliographic sources see references.

1. Lankester (1870, p. 410): Thorpe, Snape, Stow Bardolf and Herrimere
2. Davidson (1874, p.111): Gisleham, Thorpe, Stow Bardolf, Downham,
Ely and Feltwell.
3. Teall (1875, pp. 22-23): Hillgay and Southery.
4. Keeping (1883, pp. 35-37): West Dereham, Cotton, Hardwick and Herrimere.
5. Ager (1971, pp. 393, 397): King's Lynn and Thetford Warren.
6. Casey (1973, pp. 208, 209, 211, 230): Letchworth, Highgate and Leziate.
7. British Museum (Natural History) Collection: Epping Bus Station.
8. Norwich Castle Museum: Southery, Soham Tracey, Reveningham (location
not traced) and Leziate.
9. Own observations: Leziate, Stockton.

Appendix 3.

Bivalves recorded from the Spilsby Sandstone 1867-1912

<div>Source</div> <div>Taxa</div>	Judd 1867	Keeping 1882	Jukes-Browne 1887	Ussher, Jukes-Browne & Strahan 1888	Woods 1899-1912
<u>Cucullaea donningtonensis</u> Keeping		x	x	x	x
<u>Cucullaea vagans</u> Keeping			x	x	?
<u>Avicula</u> sp.		x		x	
<u>Pecten Cottaldinus</u> d'Orbigny		x		x	
<u>Pecten orbicularis</u> Sow.		x	x		x
<u>Pecten orbicularis</u> var. <u>magnus</u> Keep.			x	x	
<u>Pecten cinctus</u> Sow				x	
<u>Inoceramus neocomiensis</u> d'Orb			x		
<u>Inoceramus</u> sp.		x		x	x
<u>Aucella volgensis</u> Lahusen					x
<u>Lithodomus</u> sp.		x		x	
<u>Pinna</u> sp	x		x		
<u>Lima tombeckiana</u> d'Orbigny			x	x	
<u>Lima</u> sp.			x		
<u>Trigonia alaeformis</u> Sow. var.				x	
<u>Trigonia ingens</u> Lycett		x		x	x
<u>Trigonia Keepingi</u> Lycett		x		x	
<u>Trigonia robinaldina</u> d'Orbigny			x	x	
<u>Trigonia Tealbyensis</u> Lycett		x	x	x	
<u>Trigonia</u> aff. <u>alina</u> Lycett			x		
<u>Trigonia</u> aff. <u>Moretoni</u> Lycett			x		
<u>Trigonia</u> sp. <u>clavelate</u> form			x		
<u>Trigonia</u> sp. <u>daedaloid</u> form				x	
<u>Lucina crassa</u> Sow.	x		?		
<u>Lucina lirata</u> Phillips			x		
<u>Cardium subhillanum</u> Leymerie		x		x	x
<u>Astarte claxbiensis</u> Woods					x
<u>Astarte</u> sp.		x	x	x	
<u>Tellina</u> sp.		x		x	
<u>Cytherca</u> sp.		x		x	
<u>Thetis</u> sp.		x		x	
<u>Corbicella claxbiensis</u> Woods					x
<u>Myacites</u> sp.		x		x	
<u>Panopea neocomiensis</u> Leymerie			x		
<u>Panopea spilsbiensis</u> Woods					x
<u>Pholadomya Martini</u> ? Forbes	x				
<u>Pholadomya</u> sp.		x		x	
<u>Thracia</u> sp. (Large)		x			
<u>Martesia constricta</u> Phillips					x
<u>Arca</u> sp		x		x	

Appendix 4.

Collecting and Preparation Techniques.

Introduction.

The principal problem when studying the Spilsby bivalve fauna is that the bulk of the fauna is preserved as natural moulds in calcareous, phosphatic and sideritic concretions. Linsley (1965) has stressed the importance of collecting such moulds. It was necessary to adapt existing moulding techniques for making casts from the natural moulds. The high relief with undercuts on many specimens ruled out rigid casting materials and the most suitable technique involved the use of flexible cold cure silicone silastomer rubbers.

Collecting.

Specimens were normally collected in bulk. The richly fossiliferous phosphatised concretions (up to 200 mm diameter) of the Basal Spilsby Nodule Bed were dug out from in situ by spade and roughly concentrated by hand screening (both wet and dry) using a $\frac{1}{4}$ " garden seive - a crude but effective version of McKenna's (1962) techniques. The concentrate was transported in 40 kg sacks, then left to soak for at least 24 hours in plastic dustbins filled with hot water and industrial detergent (Teepol). In the laboratory the concentrate was further cleaned by scrubbing in hot water and detergent, and screened to 3-4 mm. The finer fractions were examined but only contained indeterminate and fragmentary specimens. Finally the fossils were hand picked from the cleaned and dry nodules. Large nodules were broken open by hammer to collect from the interiors.

Calcareous concretions up to 2 m in diameter were extracted and broken

open in the field using pick axe (a shorter bladed mattock is useful for extraction from quarry faces), a sledge hammer and chisels. Pieces of fossiliferous concretion (up to 60 kg) were then transported to the laboratory - the larger the piece, the less the damage to the specimens during transport.

Preparation

i. Extraction and development in matrix.

The blocks of fossiliferous rock were broken by hammer (a 2lb lump hammer with a broad head) and chisel to reveal specimens in the laboratory. As the shell of the specimen has normally gone, it is necessary to preserve the mould and it is important to remember to keep external and internal parts of a mould together. To economise on the volume retained to support the natural mould, trimming was done on a 10" diamond saw in preference to a jaw breaker which frequently causes damage to specimens. The saw blade is mounted vertically projecting through a slit in a flat bench with guards to protect user. The block to be cut can be safely hand held and trimmed very close to the specimen. Although the saw is normally used with coolant, small fragile specimens in soft matrix can be cut dry. Large specimens were cut on an 18" diamond blade and not hand held.

Small pieces of matrix were removed from specimens using a Consolidated Pneumatic CP61 Air Scribe running on compressed air at 40-80 psi. This pneumatic chisel is very precise and has variable intensity. A fixed intensity tool, the Desoulter VP 2/06887 is of rather less precision. The electrically operated Burgess Vibrotool VT.62 is not very satisfactory despite its variable control and tended to damage the surface of specimens. The air operated tools held just above the surface of the specimen generally

cause a very clean break between matrix and specimen. The jet of air also immediately blows away the dust and waste rock which the electric tool fails to do. For some very delicate preparation a Dentsply Cavitron was used successfully. Removal of fine adhering matrix deep in crevices was achieved with ultrasonic techniques.

Fragile and porous specimens were hardened using Butvar. A high degree of penetration was achieved by drying the specimens in an oven at about 80-100°C and then immediately immersing in a dilute solution of Butvar. Broken specimens were repaired using a thick solution of Butvar, Eastman 910 instant adhesive or water soluble Unibond.

ii. Casting Materials.

Until recently latex rubber (Rixon 1976, summarises use), with its high degree of shrinkage, and Vinamold were the principal flexible casting and moulding materials. Vinamold, despite its cheapness and reusability (see Percy 1965 for details of properties), was objectionable to use and did not provide a high degree of reproduction. The general use of these and other materials is given in Kummel and Raup (1965), Allman and Lawrence (1972) and Rixon (1976). Despite its expense, the most satisfactory material used in the study of the Spilsby fauna has been cold cure silicone silastomer compounds. The quality of reproduction is excellent. The casts shrink by a negligible amount compared to latex and have a better life expectancy (Rigby and Clark 1965). The maximum shrinkage measured here has been 2%.

3. Silastic 504 RTV (Tiranti 1972).

This is a red opaque thixotropic (i.e. non flowing) rubber with

a working time of 5 minutes to 8 hours, and a cure time of 15 minutes to 48 hours depending on the catalyst proportion. Although the flexibility and tear strength are slightly less than for 9161, the precure thixotropic state allows special field use. It can be used on surfaces of any orientation, even vertical or overhanging. Thus uncollectable specimens can be recorded permanently, quickly and economically by using only a thin skin cast.

iii Method of casting.

The surface of the specimen to be cast must be clean, dry and hardened with Butvar. Cracks should be filled (see Rixon 1976, p. 205). A coffer dam of plasticine with card or thin metal sheet is constructed around the specimen sufficiently high to allow complete coverage. Plasticine and specimen are then painted with a thin coat of Teepol sufficient not to obscure fine surface detail. This allows easy separation of cast and mould. The required silicone rubber is mixed with catalyst and a thin film is painted with a brush (fig.a) over the whole specimen, and then the rest of the rubber is poured on avoiding the formation of bubbles until the specimen is covered (fig. b). After setting, the plasticine is removed and the cast carefully eased off the mould.

Difficulty is encountered when casting from very high relief moulds with undercuts eg. hinge lines and highly tuberculate ornament. Either the silicone rubber breaks off in the mould, or air bubbles obscure the fine detail. For such specimens Silastic G is often the most satisfactory casting material. The technique is basically that just described, but to avoid bubbles (which form more readily in Silastic G because of its greater viscosity), the walls of the coffer dam should be constructed about 5x the required height to cover the specimen. Once the rubber has been poured

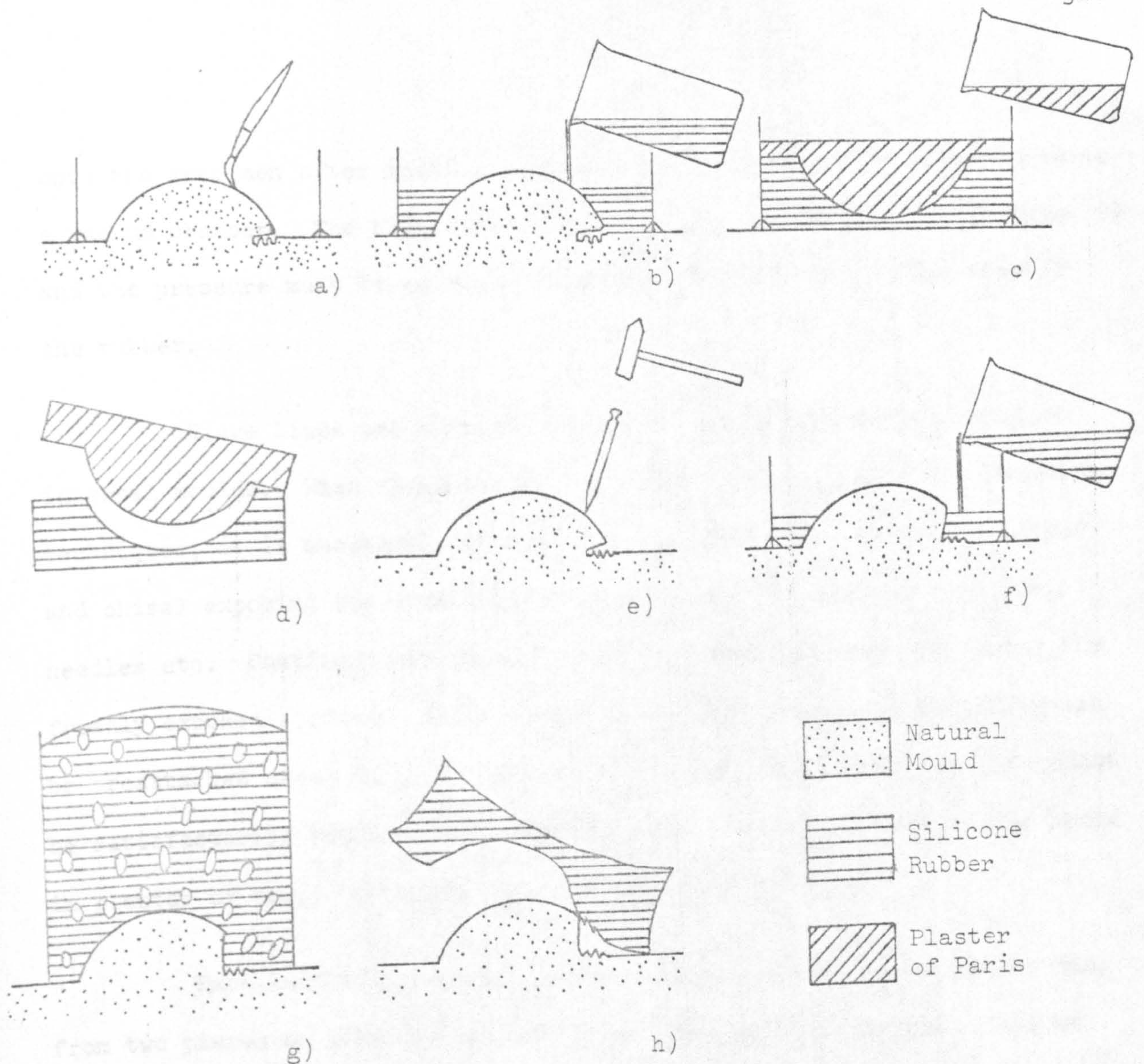


Figure 1.

Stages in the preparation of casts from natural moulds using silicone rubber. See text for description.

onto the specimen after initial painting etc. it should be transferred to a vacuum chamber. The high coffer walls retain the frothing fluid (fig. 9) and the pressure must be released before the end of the working time of the rubber.

Hinge lines are commonly obscured by the umbonal infilling on internal moulds. When these cannot be cleaned by ultrasonic and brushing techniques, it is necessary to break off the umbo (fig. e) with a hammer and chisel exposing the dentition and allowing cleaning with cavitron, needles etc. Casting then proceeds in the normal way after hardening the freshly exposed surface. After casting, the broken umbonal infilling can be reattached using Unibond. Umbonal infillings that are sawn off cannot be satisfactorily replaced. An alternative is to make a cast of the mould in plaster of paris to record original shape (figs. c, d).

Excellent silicone rubber casts of the actual shell can be made from two pieces or multiple moulds, e.g. the complete external mould of paired valves in occlusion or the internal and external mould of a single valve. The two or more parts are prepared in the normal way and coated with the rubber. When the rubber is nearing the end of its working time it becomes more viscous and at this stage it should be quickly piled up on the surface of each piece and then the parts brought together ensuring that no air bubbles are trapped. Excess rubber squeezes out of the cracks. Some bubbles may remain trapped but if the specimen is allowed to set with the least important area of the specimen pointing upwards, the bubbles may then accumulate in a place of little significance.

Broken or split silicone rubber moulds can be repaired using Dow Corning Silastic 732 RTV (readily available in hardware shops as

bathroom sealant).

Economy.

Despite their expense (c£40 per 2 litres) silicone rubbers can be used economically. They can be used as thin skins with either plaster of Paris backing or embedded with gauze for strengthening. Excess rubber can be trimmed off specimens and reject casts can be cut up and used as fill in further specimens.

Suppliers of equipment and materials.

Pneumatic hammers:

- 1) Consolidated Pneumatic Co. Ltd.,
282 Dawes Road,
London SW6.
- 2) Desoulter Bros. Ltd.,
The Hyde,
Hendon,
London NW9.

Silastic Rubbers and Vinamold:

- 1) Alec Tiranti Ltd.,
70 High Street,
Theale,
Berks, England.

Silastic 9161 from:

Hopkins and Williams,
Chadwell Heath,
Essex, England.

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Blandford Press, London 335 pp. 180 figs. 9 pls.

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Freeman, San Francisco and London. 852 pp.

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Percy, H.M. 1965. New Materials in Sculpture. 2nd Ed. Tiranti,

London. 152pp. 99 figs.

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and Raup, D. Eds. (see above) pp 389-413, 2 figs.

Rixon, A.E., 1976, Fossil Animal Remains. Their Preparation and Preservation.

Athlone Press, London. 304pp. 13 pls. 34 figs.

Tiranti, A. Ltd. 1972. Cold cure Silastic 3110, 504, G and 732.

Tiranti Ltd. London. 13 pp. 21 figs.

Appendix 5.

Draft application to ICZN to vary the type species of the subgenus Dicranodonta Woods (1899) (Mollusca, Bivalvia).

Woods (1899, p. 53) proposed Cucullaea donningtonensis Keeping (1883) as type species of Dicranodonta, a new subgenus of Cucullaea.

The holotype came from a remanie horizon, the Black Grit Nodules, at the base of the Lower Greensand of Upware, Cambridgeshire, and is believed to be reworked from a Middle Volgian to Ryazanian deposit.

In the original diagnosis of Cucullaea (Dicranodonta), Woods (1899, p. 53) states: 'Shell stout, subquadrate or rounded. Hinge area broad. Hinge plate large, curved; central teeth transverse; lateral teeth long, curved ventrally, nearly parallel, often bifurcating. No posterior adductor plate.' This diagnosis clearly refers to the robust specimens that he figured as C. (D.) donningtonensis of the Claxby Ironstone of Benniworth Haven, Lincs, and which are believed to be of Valanginian age. Subsequently these specimens have been regarded as typical C. donningtonensis (eg. Wilson, 1948 and Castell, 1962). However specimens of true C. donningtonensis from the Black Grit Nodules and also from the Spilsby Sandstone and contiguous deposits up to S. stenomphalus Zone, have a smaller hinge plate and the lateral teeth, although subparallel, do not bifurcate.

The specimens which Woods used in his diagnosis are here renamed C. (D.) benniworthensis: the specimen which he figured (1899, pl. 10, fig. 14) is proposed as holotype and is preserved in the Sedgwick Museum, (SMC B.11222). To enable Dicranodonta to be used in the sense intended by Woods, it is proposed that C. (D.) benniworthensis nom. nov. be made the type species of Dicranodonta.

Appendix 6.

Bulk Faunal Analyses.

This appendix records the basic information from which the quantitative results of chapter 4 were obtained. The amount of information was kept to a minimum to enable simple studies to be made as time did not allow a computer assisted study to be made as in Stirrup (1975).

The recorded taxa are listed in two groups, first the pelagic forms which do not concern this study and secondly the benthonic forms which do. They are listed in order of abundance. Column 1 records the number of isolated valves (Isol) including fragments. For bivalves this figure is halved in the second column (Real) to give a realistic number of original animals. Because of preferential preservation of some valves, eg. oysters, some figures are only reduced by .75. Column 3 records the number of associated pairs of valves (Assoc) for bivalves and the fourth column gives the total (Tot) used for calculation. Column 5 gives the percentage benthonic representation of each taxon (Ben%) and column 6 gives the cumulative percentage (Cum%). The final column records special features of association of taxa.

Bulk Faunal Analysis of the Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.
Information from authors collecting.

	Isol	Recl	Assoc	Tot	Ben%	Cum%	Association
<u>Pelagic.</u>							
Ammonites	313						
Belemnites	50						
Wood	2						
Bone (Reptile)	.1						
<u>Benthonic</u>							
Pleuromya	55	28	245	273	19.96	19.96	occluding
Grammatodon sch.	101	51	97	148	10.82	30.78	occluding
Lucina	4	2	135	137	10.01	40.79	occluding
Ostreids	81	61	56	117	8.55	49.34	occluding, ammonite xenomorphism
Hiatella i.	2	1	45				occluding in borings
Hiatella ii.	5	3	52	101	7.38	56.72	occluding free
Anisocardia	146	73	25	98	7.16	63.88	occluding
Pressastarte	63	32	15	47	3.44	67.32	occluding
Indet. bivalvia	76	38	-	38	2.77	70.09	
Plicatula	21	16	21	37	2.70	72.79	occluding, ammonite xenomorphism
Serpulid	33	33	1	34	2.49	75.28	attached inside Pleuromya
Bathrotomaria	31	31	-	31	2.27	77.77	
Rouillieria	2	1	26	27	1.97	79.94	occluding
Hartwellia	38	19	5	24	1.75	81.49	occluding
Grammatodon comp.	25	13	8	21	1.54	83.03	occluding
Rhynchonella	1	1	20	21	1.54	84.57	occluding
Gastropod 1	19	19	-	19	1.39	85.96	
Pholadomya	6	3	16	19	1.39	87.35	occluding
Nicaniella	32	16	3	19	1.39	88.74	occluding
Myophorella	34	17	2	19	1.39	90.13	occluding
Oxytoma	23	18	-	18	1.32	91.45	
Plagiostoma	34	17	-	17	1.24	92.69	
Gastropod 2	14	14	-	14	1.02	93.71	
Camptonectes	21	11	1	12	0.88	94.59	occluding
Indet. gastropoda	12	12	-	12	0.88	95.47	
Entolium smooth	14	17					
Entolium grooved	6	3	1	11	0.80	96.27	occluding
Modiolus	4	2	4	6	0.39	96.66	occluding
Camptochlamys	8	4	1	5	0.37	97.03	occluding
Grammatodon prod.	8	4	1	5	0.37	97.40	occluding
Girardotia	7	4	1	5	0.37	97.77	occluding inside pleuromya
Pinna	3	2	3	5	0.37	98.14	occluding
Serpulid	4	4	-	4	0.29	98.43	
Gastrochaena	-	-	3	3	0.22	98.65	occluding in boring
Gastropod 3	3	3	-	3	0.22	98.87	
Naticid	3	3	-	3	0.22	99.09	
Thracia	1	1	2	3	0.22	99.31	occluding
Neocrassina	4	2	-	2	0.15	99.46	
Trautscholdia	3	2	-	2	0.15	99.61	
Gastropod 4	2	2	-	2	0.15	99.76	
Pseudolimea	2	1	-	1	0.073	99.83	
Placunopsis	-	-	1	1	0.073	99.90	ammonite xenomorphism
Gresslya	-	-	1	1	0.073	99.98	occluding
Cucullaea	2	1	-	1	0.073	100.06	
Bryozoan	-	-	1	1	0.073	100.13	interior of gastropod
Lingula	1	1	-	1	0.073	100.20	

Bulk Faunal Analysis of erratic blocks of Lower Spilsty Sandstone, P. oppressus
Zone, Middle Volgian, Leziate, Norfolk.

Information from IGS Collection.

	Isol	Recl	Assoc	Tot	Ben%	Cum%	Association
<u>Pelagic.</u>							
Paracraspedites	28						
Acroteuthis	35						
<u>Benthonic.</u>							
Entolium	142	71	-	71	28.06	28.66	
Rouillieria	17	9	20	29	11.46	39.52	20 occluding
Lucina	35	18	2	20	7.91	47.43	1 occluding, 1 skewed
Ostreid	23	18	-	18	7.11	54.54	
Lyapinella	24	12	6	18	7.11	61.65	2 occluding, 4 gaping
Anisocardia	30	15	2	17	6.72	68.37	1 occluding, 1 skewed
Oxytoma	19	15	-	15	5.93	74.30	
Myophorella	25	13	-	13	5.14	79.44	
Camptonectes	21	11	-	11	4.35	83.79	
Pleuromya	3	2	5	7	3.77	86.56	5 occluding
Cucullaea	12	6	1	7	2.77	89.33	1 gaping
Pressastarte	12	6	-	6	2.37	91.70	1 occluding
Pinna	3	2	1	3	1.18	92.88	
Serpula	3	-	-	3	1.18	94.06	
Nicaniella	4	2	-	2	0.79	94.85	
Falciomytilus	2	1	1	2	0.79	95.64	1 occluding
Senis	3	2	-	2	0.79	96.43	
Gastropoda indet.	2	-	-	2	0.79	97.22	
Placunopsis	1	-	-	1	0.39	97.61	
?Plicatula	1	-	-	1	0.39	98.00	
Arctotis	1	-	-	1	0.39	98.39	
Grammatodon	1	-	-	1	0.39	98.78	
Musculus	1	-	-	1	0.39	99.17	
Pleurotomiid	1	-	-	1	0.39	99.56	
Gastropod 2	1	-	-	1	0.39	99.95	

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Bulk Faunal Analysis of Bed 1 concretions, Lower Spilsby Sandstone, S. preplicomphalus
Zone, Upper Volgian, West Keal, Lincs.

Information from author's collecting.

	Isol	Recl	Assoc	Tot	Ben%	Cum%	Association
<u>Pelagic.</u>							
Ammonites	40						
<u>Benthonic.</u>							
Entolium smooth	670						
Entolium grooved	4	337	-	337	50.68	50.68	
Indet. bivalvia	100	100	-	100	15.03	65.71	
Sowerbya	61	32	1	33	4.96	70.67	occluding
Pleuromya	23	12	20	32	4.81	75.48	occluding, vertical
Procyprina	59	30	1	31	4.66	80.14	occluding
Lyapinella	41	21	7	28	4.21	84.35	gaping, skewed
Lucina	30	15	5	20	3.01	87.36	occluding, skewed, gaping
Myophorella teal.	35	18	-	18	2.71	90.07	
Pinna	7	4	7	11	1.65	91.72	occluding vert & horiz
Protocardia	14	7	1	8	1.20	92.92	gaping
Gastropod 1	-	-	7	7	1.05	93.97	inside vertical Pinna
Pressastarte	11	6	-	6	0.90	94.87	
Indet. gastropoda	6	-	-	6	0.90	95.77	
Cucullaea	10	5	-	5	0.75	96.52.	
Myophorella int.	7	4	-	4	0.60	97.12	
Trautscholdia	6	3	-	4	0.45	97.57	
Camptonectes	4	2	-	2	0.30	97.87	
Musculus	1	1	1	2	0.30	98.17	occluding, skewed
Anopaea	1	1	1	2	0.30	98.47	occluding, horizontal
Patellid	2	-	-	2	0.30	98.77	
Nicaniella s.s.	1	1	-	2	0.15	98.92	
Goniomya	1	1	-	1	0.15	99.07	
Exogyrid	1	1	-	1	0.15	99.22	
Falsimyrtilus	1	1	-	1	0.15	99.37	
Corbicella	1	1	-	1	0.15	99.52	
Pseudolimea	1	1	-	1	0.15	99.67	
Modiolus	-	-	1	1	0.15	99.82	occluding horizontal
Pholadomya	-	-	1	1	0.15	99.97	occluding vertical
				665			

Bulk Faunal Analysis, Bed 6 concretions, Lower Spilsby Sandstone, S. lamplughii
Zone, Upper Volgian, Nettleton, Lincs.

Information from author's collecting.

	Isol	Recl	Assoc	Tot	Ben%	Cum%	Association
<u>Pelagic.</u>							
S. lamplughii	20						
Acroteuthis	15						
Saurian	1						
<u>Benthonic.</u>							
Entolium smooth	92	66	2	68	57.62	57.62	occluding horizontal
Entolium grooved	40						
Lyapinella	15	8	3	11	9.32	66.94	gaping
Sowerbya	7	4	-	4	3.38	70.32	
Lucina	6	3	1	4	3.38	73.70	occluding, vertical
Pinna	3	2	2	4	3.38	77.08	
Heterodont indet.	6	3	1	4	3.38	80.46	
Myophorella	6	3	-	3	2.54	83.00	
Anopaea	3	2	1	3	2.54	85.54	occluding, horizontal
Pholadomya	1	1	2	3	2.54	88.08	occluding, vertical
Corbicella	4	2	-	2	1.69	89.77	
Camptonectes	4	2	-	2	1.69	91.46	
Pressastarte	3	2	-	2	1.69	93.15	
Pleuromya	2	1	1	-	1.69	94.84	occluding, horizontal
Ostreid	1	1	1	2	1.69	96.53	cemented on Lyapinella
Oxytoma	2	2	-	2	1.69	98.22	
Gastropod 1	2	2	-	2	1.69	99.91	
				118			

Bulk Faunal Analysis of Subcraspedites Band, S. lampluzhi Zone, Upper Volgian
West Dereham Flood Relief Channel, Norfolk.

Information from IGS collection.

	Isol	Recl	Assoc	Tot	Ben%	Cum%	Association
<u>Pelagic.</u>							
Ammonites	506						
Belemnites	21						
Fish vertebrae	16						
Reptile vertebrae	15						
Large bones	77						
Fish teeth	2						
Wood	14						
<u>Benthonic.</u>							
Lyapinella	43	22	164	182	44.83	44.83	138 occluding, 24 gaping
Cucullaea	101	52	18	70	17.24	62.07	12 occluding, 6 gaping
Anisocardia	6	3	24	27	6.65	68.72	20 occluding, 4 skewed
Pleuromya	2	1	23	24	5.91	74.63	23 occluding; .
Hartwellia	12	16	18	24	5.91	80.54	14 occluding, 4 skewed
Myophorella	24	12	5	17	4.19	84.73	
Indet. bivalvia	19	10	7	17	4.19	88.92	6 occluding, 1 skewed
Discoloripes	2	1	8	9	2.22	91.14	3 occluding, 8 skewed
Martesia	-	-	6	6	1.48	92.62	6 in borings
Indet. gastropoda	6	6	-	6	1.48	94.10	
Corbicellopsis	2	1	4	5	1.23	95.33	4 occluding
Isognomon	3	2	3	5	1.23	96.56	3 occluding
Pholadomya	1	1	2	3	0.74	97.30	2 occluding
Entolium grooved	3	2	1	3	0.74	97.04	1 occluding
Entolium smooth	1						
Pleurotomariid	3	3	-	3	0.74	98.78	
Crustacean	2	2	-	2	0.49	99.27	
Myoconcha	-	-	1	1	0.25	99.52	1 skewed
Carditid	1	1	-	1	0.25	99.77	
Camptonectes	2	1	-	1	0.25	100.02	
				406			

Bulk Faunal Analysis of nodules immediately above Subcraspedites Band, Lower Mintlyn
Beds, H. kochi Zone, West Dereham Flood Relief Channel, Norfolk.

Information from IGS Collection.

	Isol	Recl	Assoc	Tot	Ben%	Cum%	Association
<u>Pelagic.</u>							
Hectoroceras	10						
Fish vertebra	1						
<u>Benthonic.</u>							
Entolium	190	85	-	85	57.43	57.43	
Anisocardia	65	33	3	36	24.32	81.75	3 occluding
Nicaniella	50	25	-	25	16.89	98.64	1 occluding
Oxytoma	2	1		1	0.68	99.32	
Tellinid	-	-	1	1	0.68	100.00	
				148			

Bulk analysis of Hectoroceras beds of clay Ironstone facies, Mintlyn Beds, H. kochi
Zone, West Dereham Flood Relief Channel, Norfolk.

Information from IGS Collections.

	Isol	Recl	Assoc	Tot	Ben%	Cum%	Association
<u>Pelagic.</u>							
Ammonites	40						
Acroteuthis	50						
Wood	50						
Fish Vertebra	1						
<u>Benthonic.</u>							
Lyapinella	561	281	26	307	59.50	59.50	14 occlud. 6 gaping, 6 skew.
Anisocardia	47	24	27	51	9.88	69.38	22 occlud. (2 vert) 4 gap, 1 sk.
Pholadomya	5	3	288	31	6.01	75.39	22 occlud. (5 vert) 1 gaping.
Pleuromya	10	5	19	24	4.65	80.04	17 occluding, 2 gaping
Indet. bivalvia	31	16	2	18	3.49	83.53	2 occluding
Myophorella	32	17	-	16	3.10	86.63	
Thracia	7	4	7	11	2.13	88.76	5 occluding, 2 gaping
Entolium smooth	17						
Entolium grooved	5	11	-	11	2.13	90.89	
Serpulid	9	-	9	9	1.74	92.63	9 inside Lyapinella
Sowerbya	11	6	2	8	1.55	94.18	2 gaping
Indet. gastropoda	7	7	-	7	1.36	95.54	
Camptonectes	9	5	-	5	0.97	96.51	
Cucullaea	4	2	2	4	0.78	97.29	1 occluding, 1 gaping
Nucula	3	2	1	3	0.58	97.87	1 occluding
Goniomya	3	2	1	3	0.58	98.45	1 gaping
Girardotia	1	1	-	1	0.19	98.64	
Anopaea	2	1	-	1	0.19	98.83	
Oxytoma	1	1	-	1	0.19	99.02	
Pressastarte	1	1	-	1	0.19	99.21	
Pseudolimea	1	1	-	1	0.19	99.40	
Totrigonia	1	1	-	1	0.19	99.59	
Crustacean	1	1	-	1	0.19	99.78	
Naticid	1	1	-	1	0.19	99.97	

Bulk Faunal Analysis of Basal Mintlyn Beds nodule bed, Borrow Pit, Constitution
Hill, West Winch, Norfolk.
Information from IGS Collection.

	Isol	Recl	Assoc	Tot	Ben%	Cum%	Association
<u>Pelagic.</u>							
Ammonites	100						
Belemnites	6						
<u>Benthonic.</u>							
Protocardia	125	63	109	172	59.51	59.51	54 occlud. 7 gaping, 48 skew.
Lyapinella	24	12	12	24	8.30	67.81	10 occluding, 2 skewed
Pleuromya	1	1	22	23	7.96	75.77	22 occluding
Corbicellopsis	8	4	10	14	4.84	80.61	10 occluding
Cucullaea	22	12	1	13	4.50	85.11	1 occluding
Gastropod 1	10	10	-	10	3.46	88.57	
Myophorella	16	8	1	9	3.11	91.68	1 occluding
Pleurotomariid	8	8	-	8	2.77	94.45	
Anisocardia	6	3	1	4	1.38	95.83	1 occluding
Sowerbya	3	2	1	3	1.04	96.87	1 occluding
Gastropod 5	2	2	-	2	0.69	97.56	
Pressastarte	1	1	1	2	0.69	98.25	1 occluding
Thracia	-	-	1	1	0.35	98.60	1 occluding
Hartwellia	-	-	1	1	0.35	98.95	1 occluding
Modiolus	-	-	1	1	0.35	99.30	1 occluding
Terebratulid	-	-	1	1	0.35	99.65	1 occluding
Entolium smooth	1						
Entolium grooved	1	1	-	1	0.35	100.00	
				289			

Bulk Faunal Analysis of Bed 6, Basal Mintlyn nodule bed, North Runcton, Norfolk.
Information from IGS Collections.

	Isol	Recl	Assoc	Tot	Ben%	Cum%	Association
<u>Pelagic.</u>							
Ammonites	44						
Belemnites	4						
<u>Benthonic.</u>							
Protocardia	40	20	21	41	48.24	48.24	20 occluding, 1 skewed
Myophorella	15	7	1	8	9.41	57.65	1 gaping
Pleuromya	1	1	6	7	8.24	65.89	6 occluding
Entolium smooth	7						
Entolium grooved	5	6	-	6	7.06	72.95	
Lyapinella	10	5	-	5	5.88	78.83	
Cucullaea	7	4	1	5	5.88	84.71	1 occluding
Indet. gastropoda	5	5	-	5	5.88	90.59	
Hartwellia	1	1	1	2	2.35	92.94	1 occluding
Indet. bivalvia	4	2	-	2	2.35	95.29	
Camptonectes	2	1	-	1	1.18	96.47	
Thracia	-	-	1	1	1.18	97.65	1 occluding
Corbicella	1	1	-	1	1.18	98.83	
Serpulid	1	1	-	1	1.18	100.01	
				84			

Bulk Faunal Analysis, Bed 10 (Casey, 1973) Mintlyn Beds, S. stenomphalus Zone,
Ryazanian, King's Lynn Bypass, Mintlyn Wood, Norfolk.

Information from IGS Collections.

	Isol	Recl	Assoc	Tot	Ben%	Cum%	Association
<u>Pelagic.</u>							
Surites	102						
Wood fragments >5mm 100's							
<u>Benthonic.</u>							
Corbula	1910	955	40	995	49.77	49.77	40 occluding
?Protocardia	1112	565	24	589	29.46	79.23	23 occluding, 1 skewed
Lyapinella	502	251	40	291	14.56	93.79	18 occlud. 12 gaping, 10 skew.
Thracia	12	6	22	28	1.40	95.19	22 occluding
Pleuromya	52	26	4	28	1.40	96.59	4 occluding
Corbicella	46	23	1	24	1.20	97.79	1 gaping
Myophorella	16	8	1	9	0.45	98.24	1 gaping
Camptonectes s.s.	16	8	-	8	0.40	98.64	
Indet. gastropods	6	6	-	6	0.30	98.94	
Ostreid	2	2	3	5	0.25	99.19	3 encrusting Boreionectes
Boreionectes	5	3	-	3	0.15	99.34	
Trautscholdia	6	3	-	3	0.15	99.49	
Girardotia	-	-	2	2	0.10	99.59	1 occluding
Entolium	4	2	-	2	0.10	99.69	
Pressastarte	2	1	-	1	0.05	99.74	
Nicaniella	2	1	-	1	0.05	99.79	
Pinna	-	-	1	1	0.05	99.84	
Nicaniella s.s.	2	1	-	1	0.05	99.89	1 occluding
Discoloripes	1	1	-	1	0.05	99.94	
Cucullaea	1	1	-	1	0.05	99.99	

PLATES

All illustrations are natural size, except where stated to be otherwise.

EXPLANATION OF PLATE 1

Figs. 1a-c, 2a-d, 3, 4, 5, 6a-c, 7a-c. Grammatodon (Grammatodon) schourovskii (Rouillier & Vossinsky). 1a-c, SRAK IG.2005, left valve; 2a-d, IG.1231, right valve; 3, IG.2131, left valve; 4, IG.1224, left valve; 5, IG.3305, right valve, all silicone rubber casts; 6a-c, IG.3319; 7a-c, IG.3317, both phosphatised steinkerns, Bed 2, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.

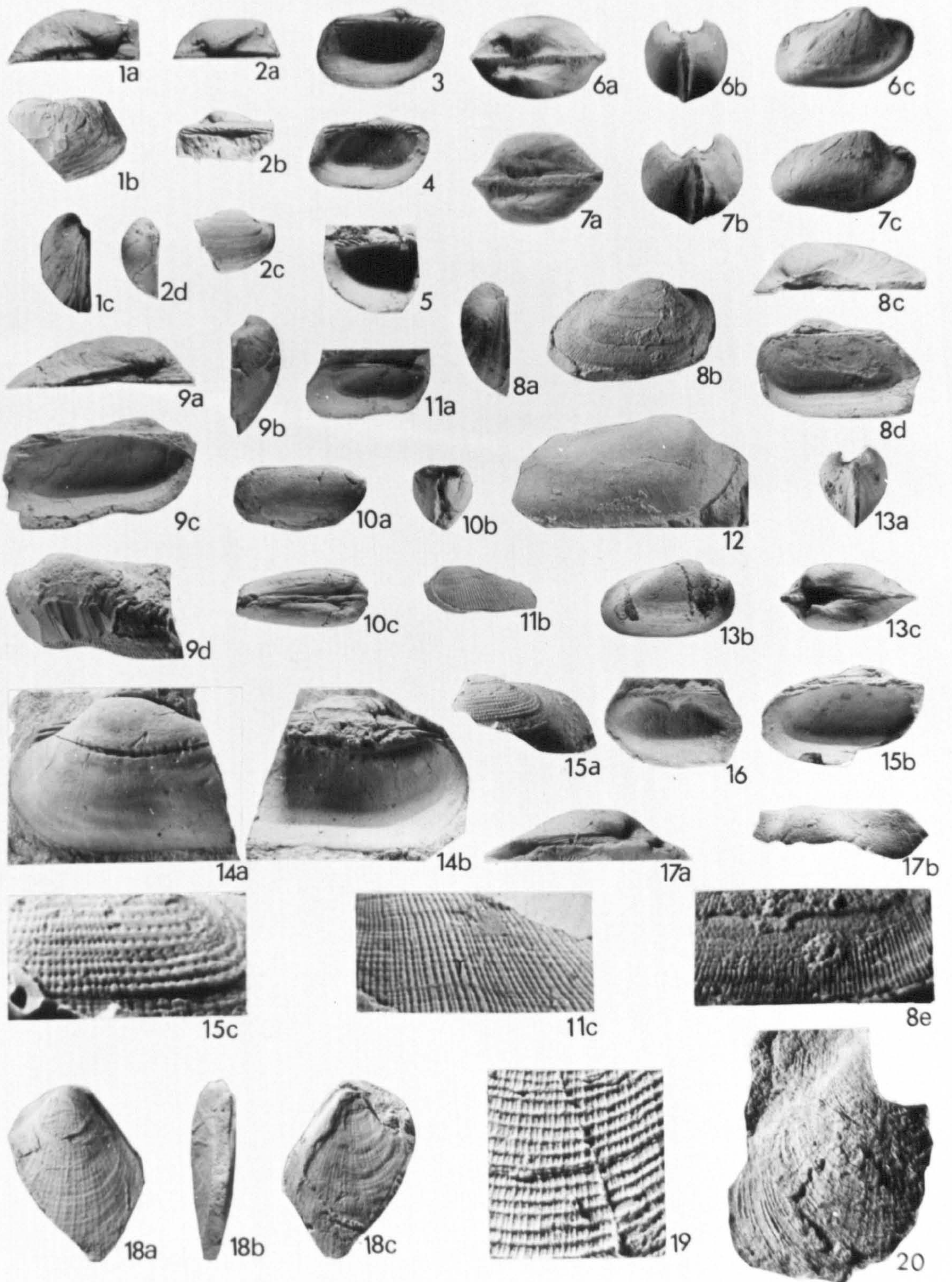
Fig. 8a-d. Grammatodon (Grammatodon) spilsbiensis sp. nov. Holotype, SRAK IG.1704, right valve, silicone rubber cast, loose block of Lower Spilsby Sandstone with S. sowerbyi, S. preplicomphalus Zone, Upper Volgian, road cutting 1km north of Spilsby, Lincs.

Figs. 9a-d, 10a-c, 11a-c, 12, Grammatodon (Cosmetodon) productum (Rouillier & Vossinsky). 9a-d, SRAK IG.2282, left valve; 11a-c, IG.2123, left valve; both silicone rubber casts, 11c showing exterior detail x3; 10a-b, SRAK IG.1404, phosphatised steinkern; 12, IG.3326, phosphatised internal mould of right valve, Bed 2, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.

Figs. 13a-c, 14a, b, 15a-c, 16, 17a, b. Grammatodon (Cosmetodon) compressiusculum (Rouillier & Vossinsky). 13a-c, SRAK IG.1237, phosphatised steinkern; 14a, b, IG.3294, 14a phosphatised internal mould of left valve, 14b, silicone rubber cast of interior; 15a-c, IG.1232, silicone rubber cast of left valve, 15c, detail of exterior x3; 16, IG.1234, silicone rubber cast of right valve; 17a, b, IG.1232, silicone rubber cast of left valve. Bed 2, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.

Figs. 18a-c, 19, 20. Camptonectes (Camptochlamys) cf. intertextus (Roemer). 18a-c, SRAK IG.2016, phosphatised steinkern; 19, IG.2013, detail of exterior ornament x3; 20, IG.1600, left valve; both silicone rubber casts, Bed 2, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.

PLATE 1

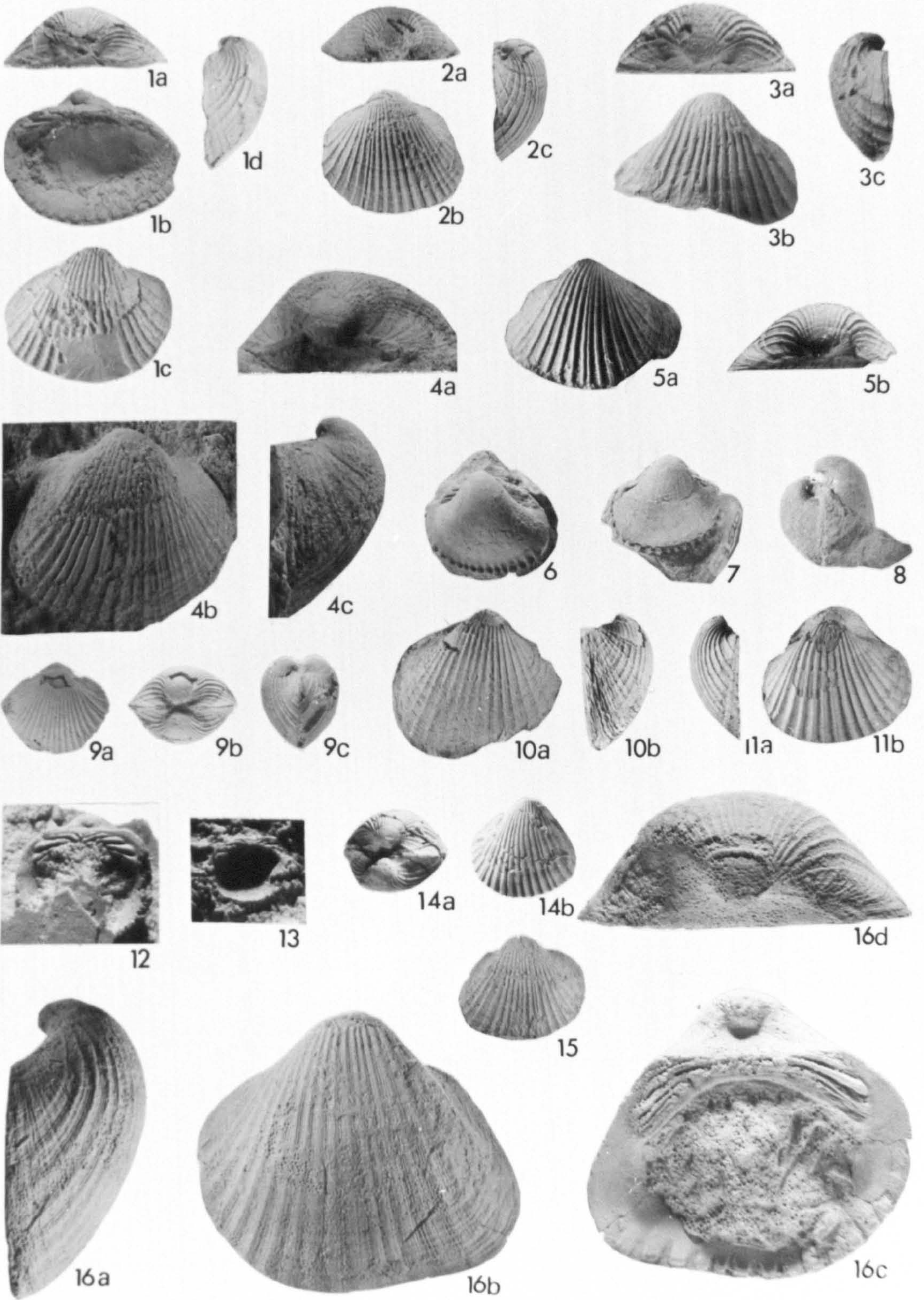


EXPLANATION OF PLATE 2

Figs. 1a-d, 2a-c, 3a-c, 4a-c, 5a, b, 6, 7, 8, 9a-c, 10a, b, 11a, b, 12, 13, 14a, b. Cucullaea (Dicranodonta) vagans Keeping. 1a-d, SMC B.27577, right valve; 3a-c, SMC B.27515, lectotype, right valve; 10a, b, SMC B.27526, holotype of C. donningtonensis Keeping (1883, pl. 8, fig. 9), right valve; 11a, b, SMC B.27524, syntype, right valve, all silicone rubber casts; 6, SMC B.27525, syntype, phosphatised steinkern, Dark Grit type nodules at base of Lower Greensand, Upware, Cambs. 2a-c, SRAK JG.1601, left valve; 9a-c, JG.1558, complete individual, Basal Shell Bed of the Muslingeelv Member, Hesteelv Formation, H. kochi Zone, Ryazanian, 3.5 km south of Crinoidbjerg, South Jameson Land, East Greenland. 4a-c, SMC B.11852, Spilsby Sandstone, Donnington, Lincs. 5a-c, LM 29/960, silicone rubber cast of right valve. No information, presumed drift of Norfolk. 7, 8, SRAK IG.520, steinkern, Lower Spilsby Sandstone, S. oppressus Zone, Middle Volgian, in erratic boulder, Bawsey Warren, Norfolk. 12, SRAK IG.2382, left valve interior x4; 13, IG.2386, right valve interior x4; both silicone rubber casts. Bed 1 calcareous concretion, Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, High Barn, West Keal, Lincs. 14a, b, IGS WA3238, silicone rubber cast of complete individual, Mintlyn Beds, H. kochi Zone, Ryazanian, West Dereham Flood Relief Channel, Norfolk.

Figs. 15, 16a-d. Cucullaea (Dicranodonta) benniworthensis sp. nov. 15, paratype, SMC. B.11221, (originally figured by Woods, 1899, pl. 10, fig. 14) right valve; 16a-d, holotype, B.11222, (originally figured by Woods, 1899, pl. 10, fig. 11) left valve, Claxby Ironstone, probably Valanginian, Benniworth Haven, Lincs.

PLATE 2



EXPLANATION OF PLATE 3

Figs. 1a, b, 2, 3, 4, 5. Anopaea brachowi (Rouillier). 1a, b, SRAK IG.1832, 1a, silicone rubber cast of hinge, 1b, internal mould of left valve, Bed 6 calcareous concretion, Lower Spilsby Sandstone, S. lamplughi Zone, Nettleton, Lincs. 2, IGS 819, internal mould of left valve; 3, IGS, 820, silicone rubber cast of umbonal region of left valve, Spilsby Sandstone, near Toynton All Saints, Lincs. 4, IGS CE 3817, internal mould of left valve; 5, CE 3052, internal mould of left valve, Mintlyn Beds, H. kochi Zone, Ryazanian, West Dereham Flood Relief Channel, Norfolk.

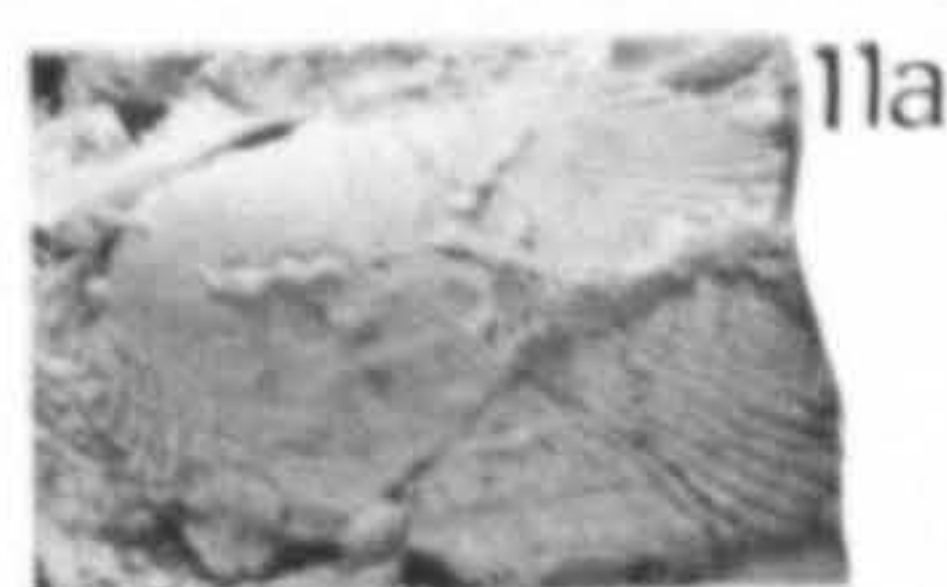
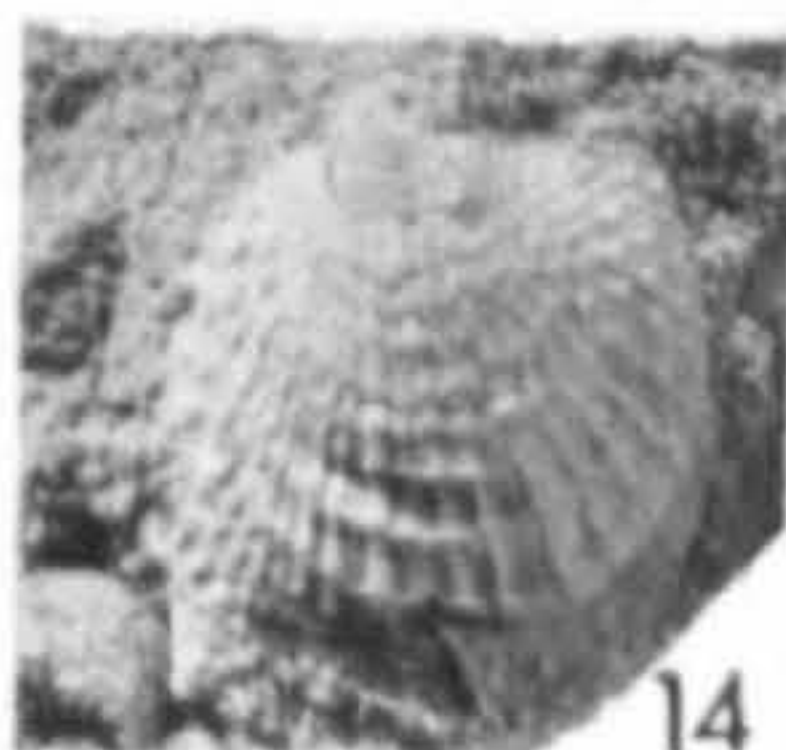
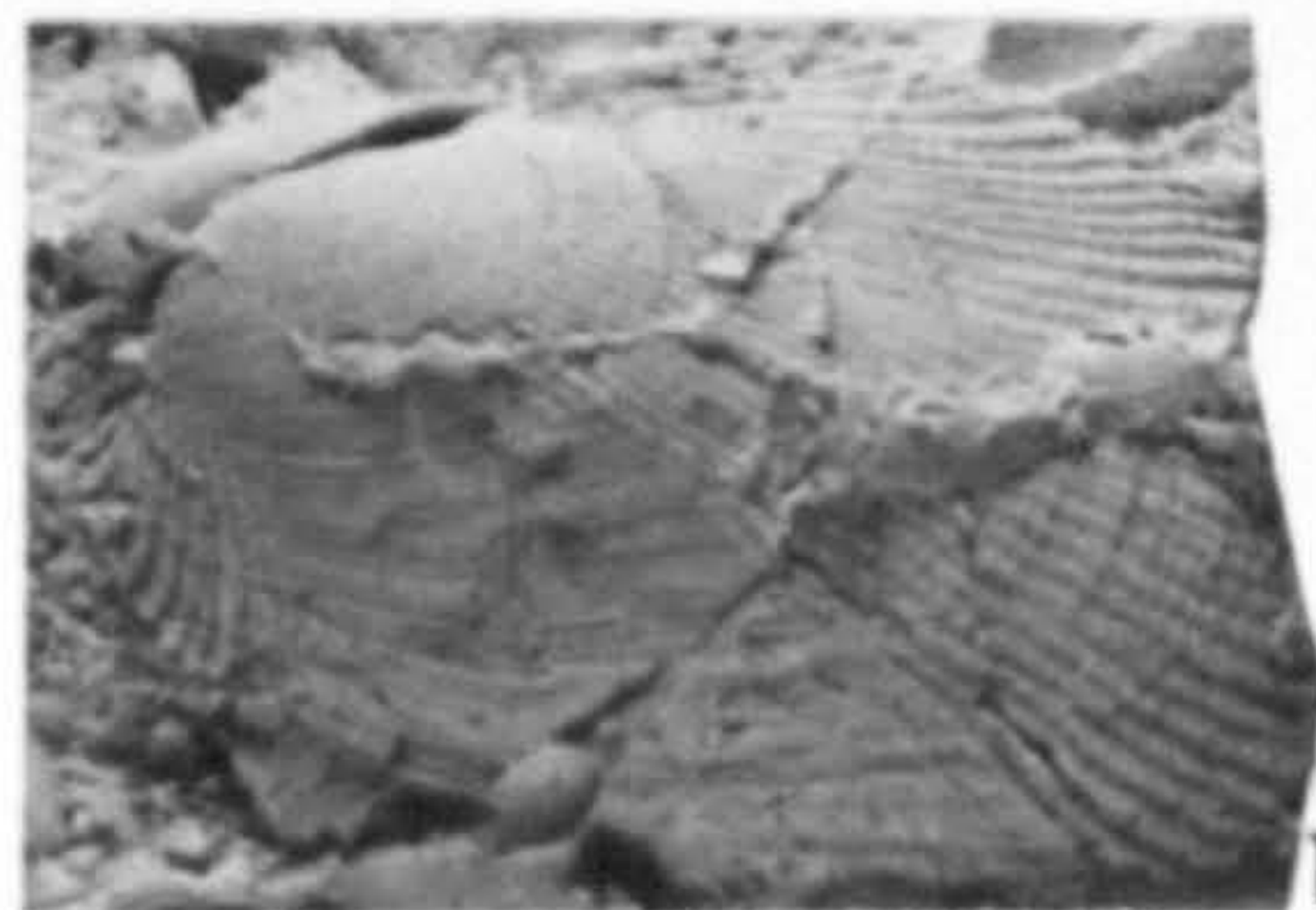
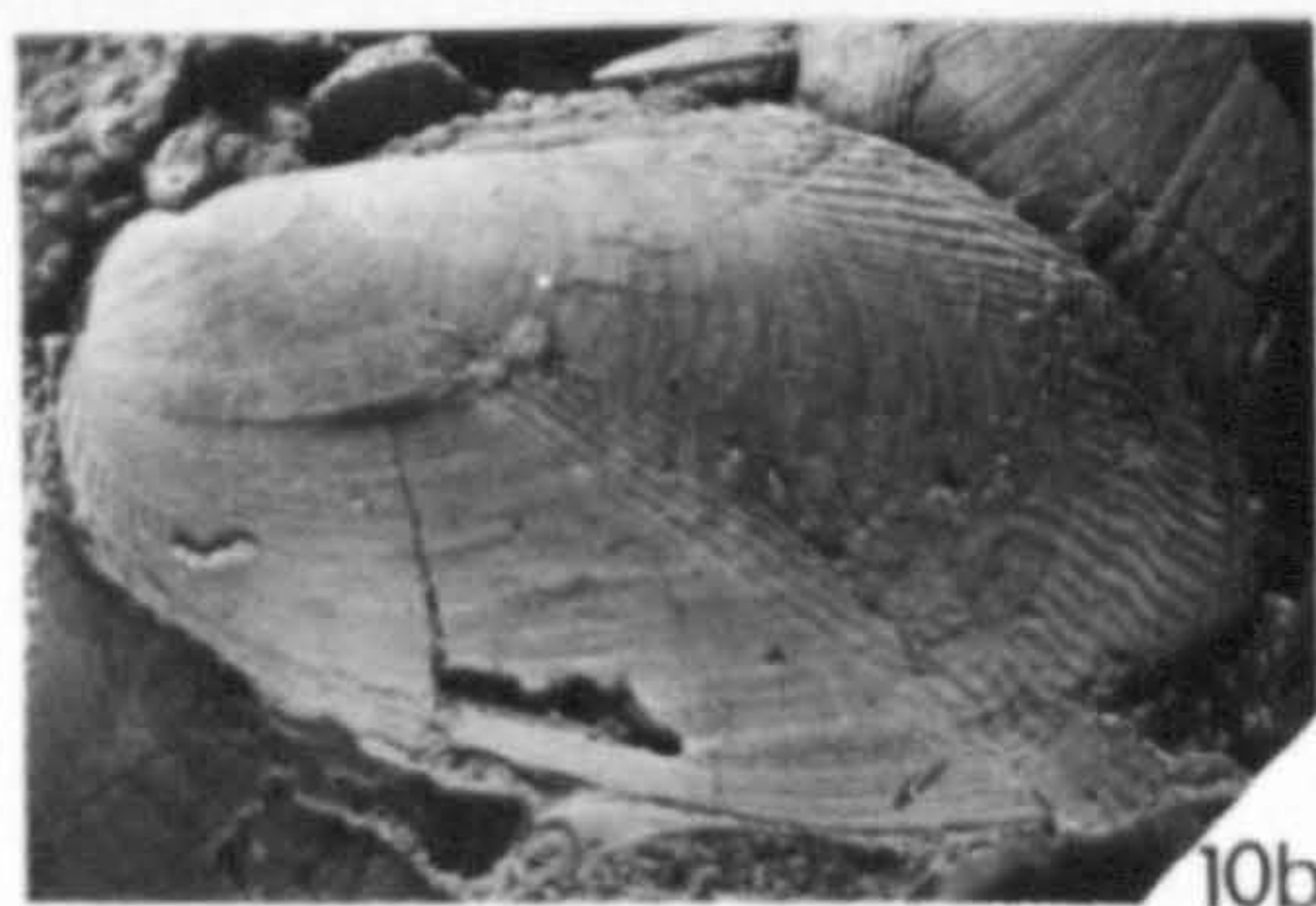
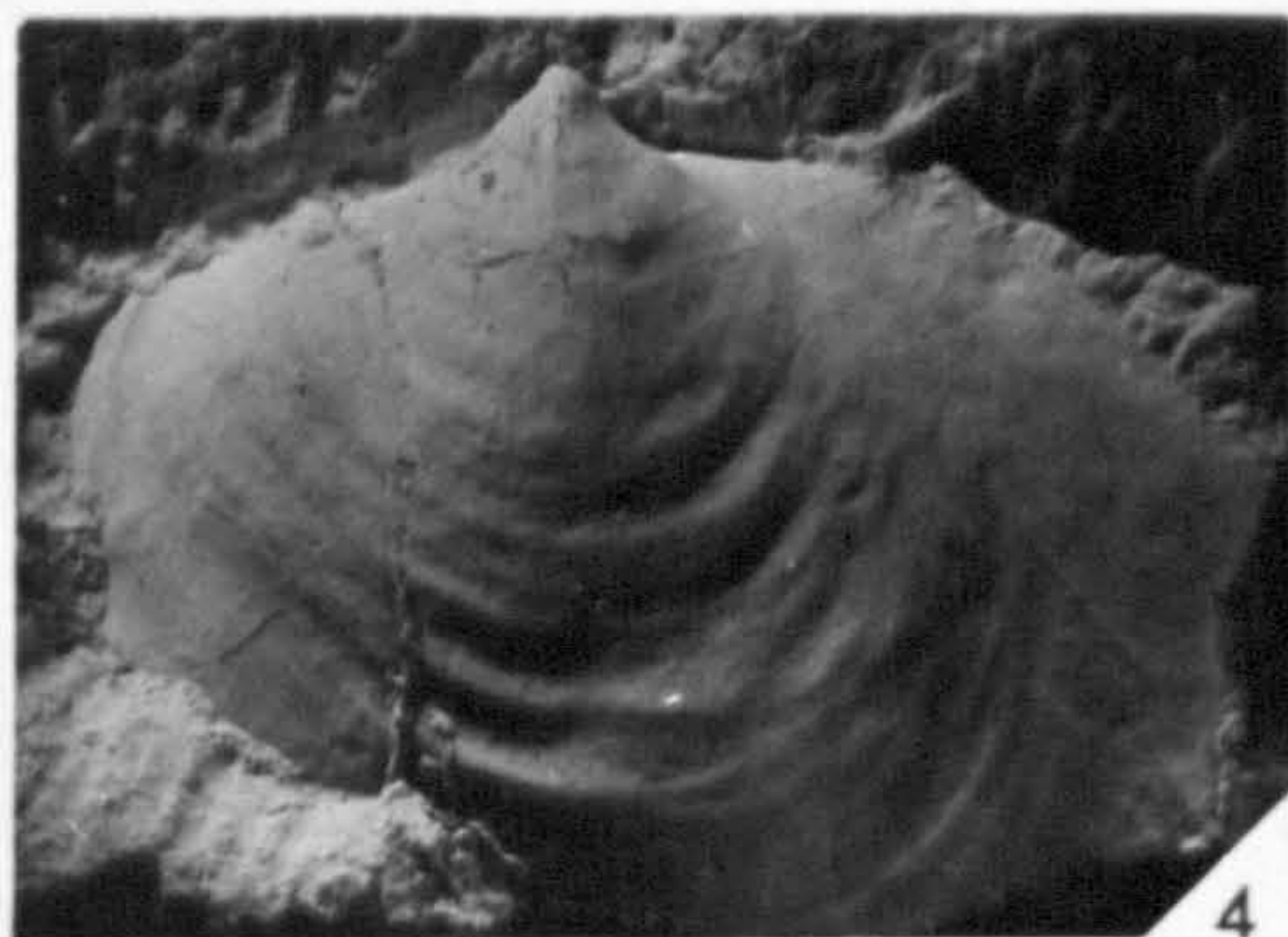
Figs. 6, 7, 8. Anopaea sphenoidea Gerasimov. 6, IGS 821, internal mould of umbonal region of right valve, Spilsby Sandstone, near Toynton All Saints, Lincs. 7, SRAK IG.2871, internal mould of left valve, Bed 1 in calcareous concretion, Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, High Barn, West Keal, Lincs. 8, IGS CE 3224, internal mould of right valve, in erratic block of Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, Bawsey Warren, Norfolk.

Figs. 9, 10a, b. Musculus (Musculus) derehamensis sp. nov. 9, IGS CE 6092-6095, paratypes; 10a, b, CE 6091, holotype, left valve, 10b x2, ?Roxham Beds, drainage Channel, Wormgay, Norfolk.

Figs. 11a, b, 12, 13a, b. Musculus (Musculus) fischerianus (d'Orbigny). 11a, b SRAK IG.2579 silicone rubber cast of left valve, 11b x2, Bed 1 calcareous concretions, Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, High Barn, West Keal, Lincs. 12, SRAK IG.1756, composite mould of left valve, erratic block of Lower Spilsby Sandstone, Middle or Upper Volgian, Bawsey Warren, Norfolk. 13a, b, IG.3390, silicone rubber cast of left valve, 13b x2, Bed 2 calcareous concretion, Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, 600m west of Harrington Hall, Lincs.

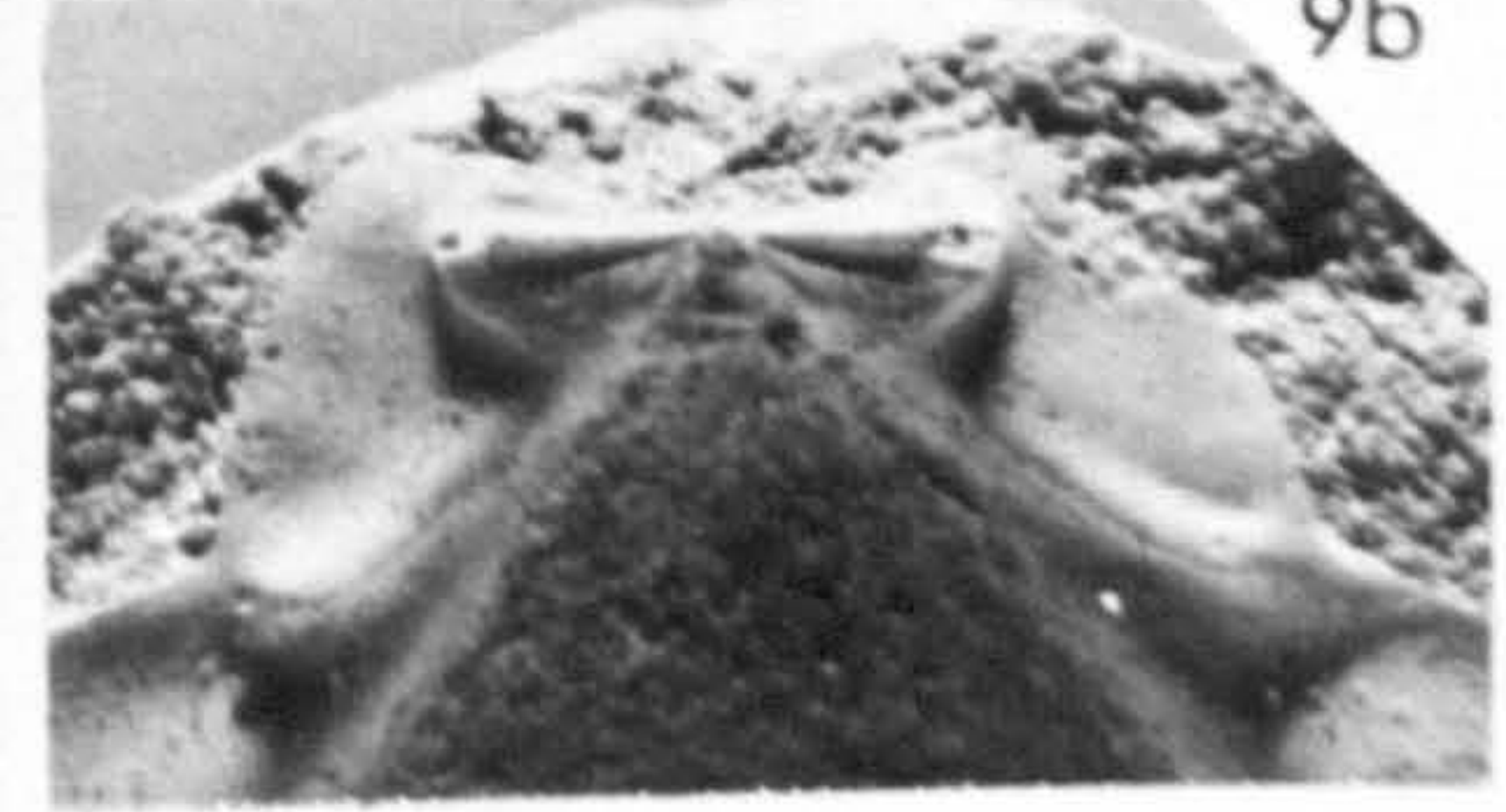
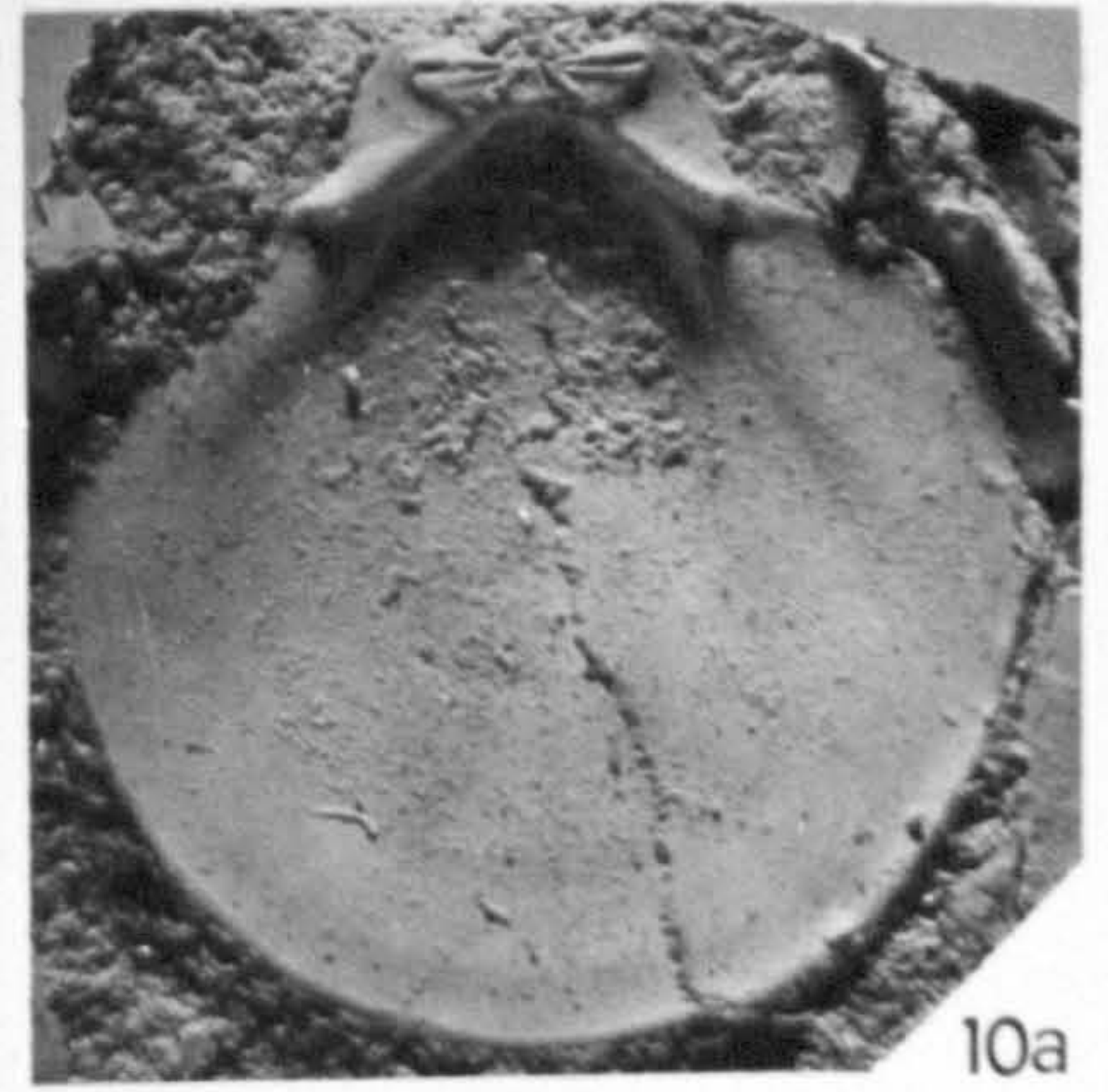
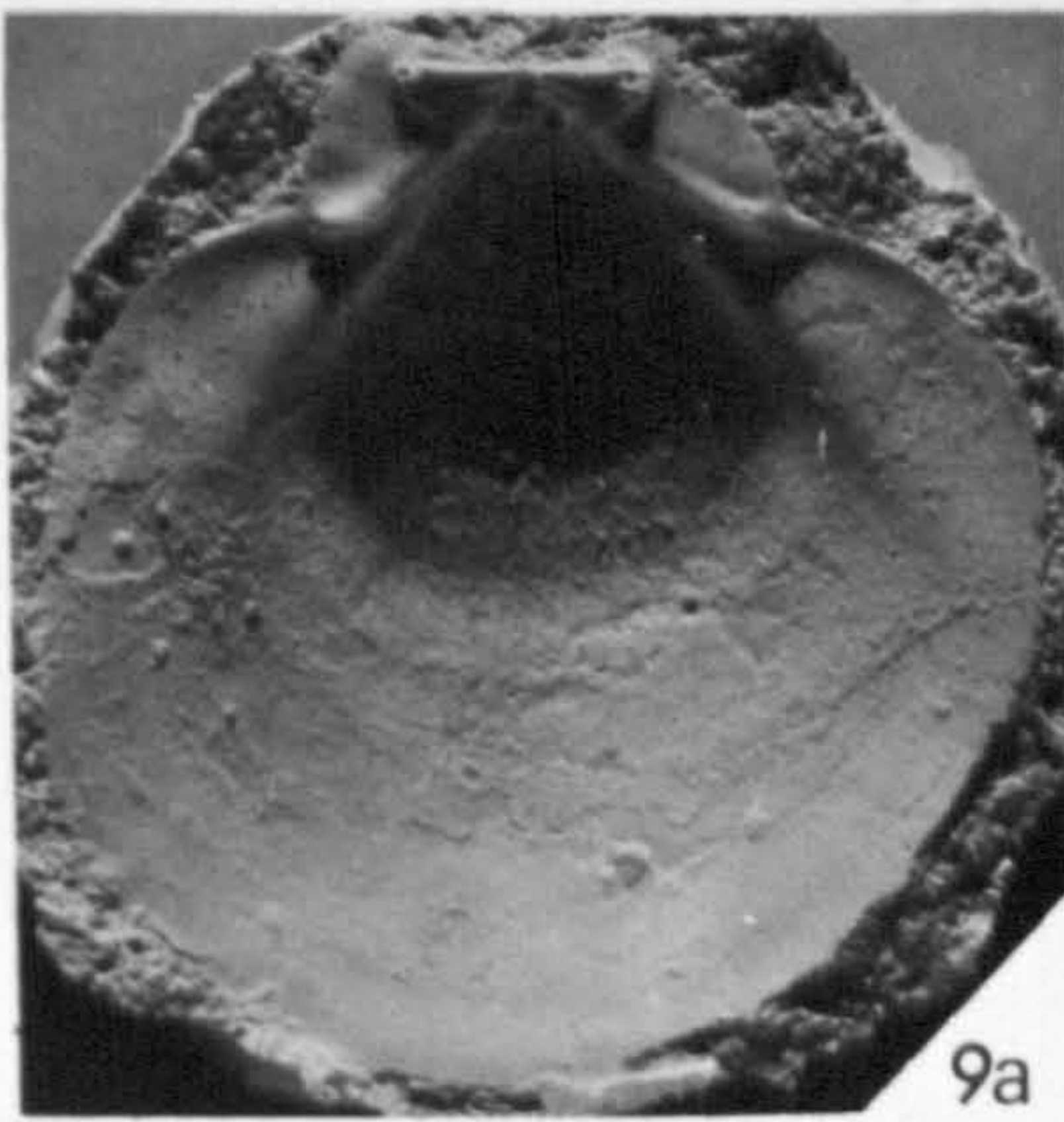
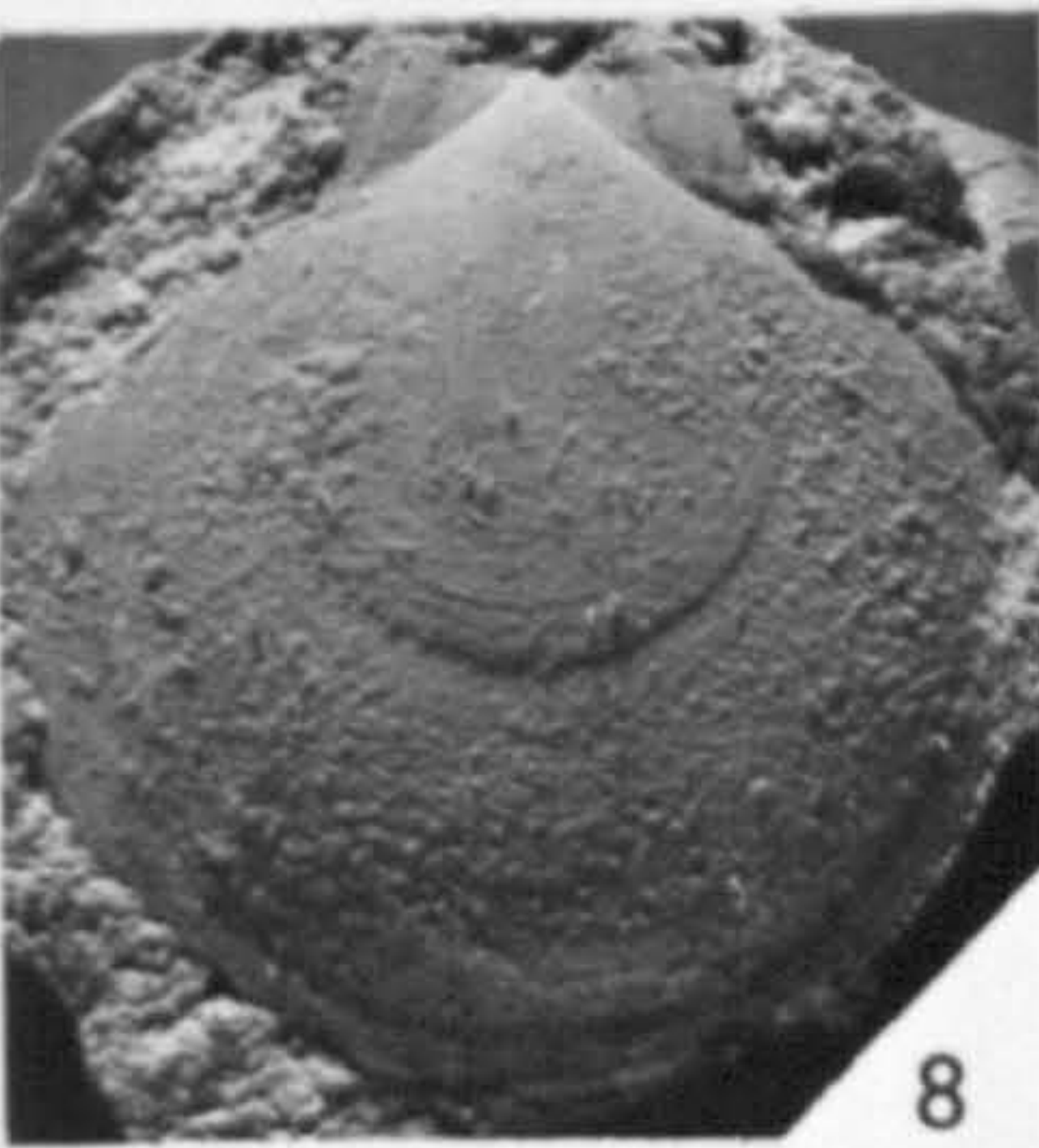
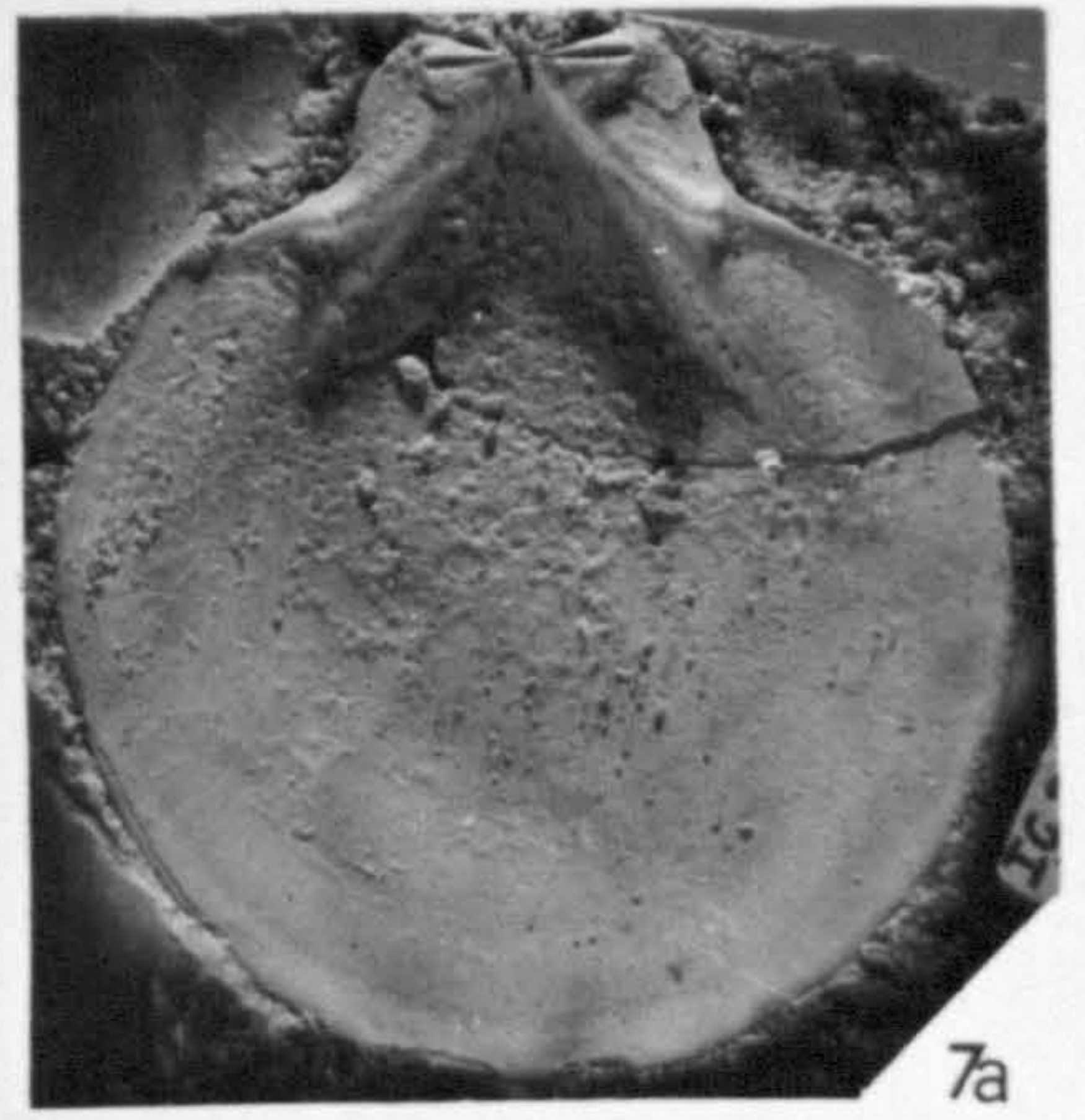
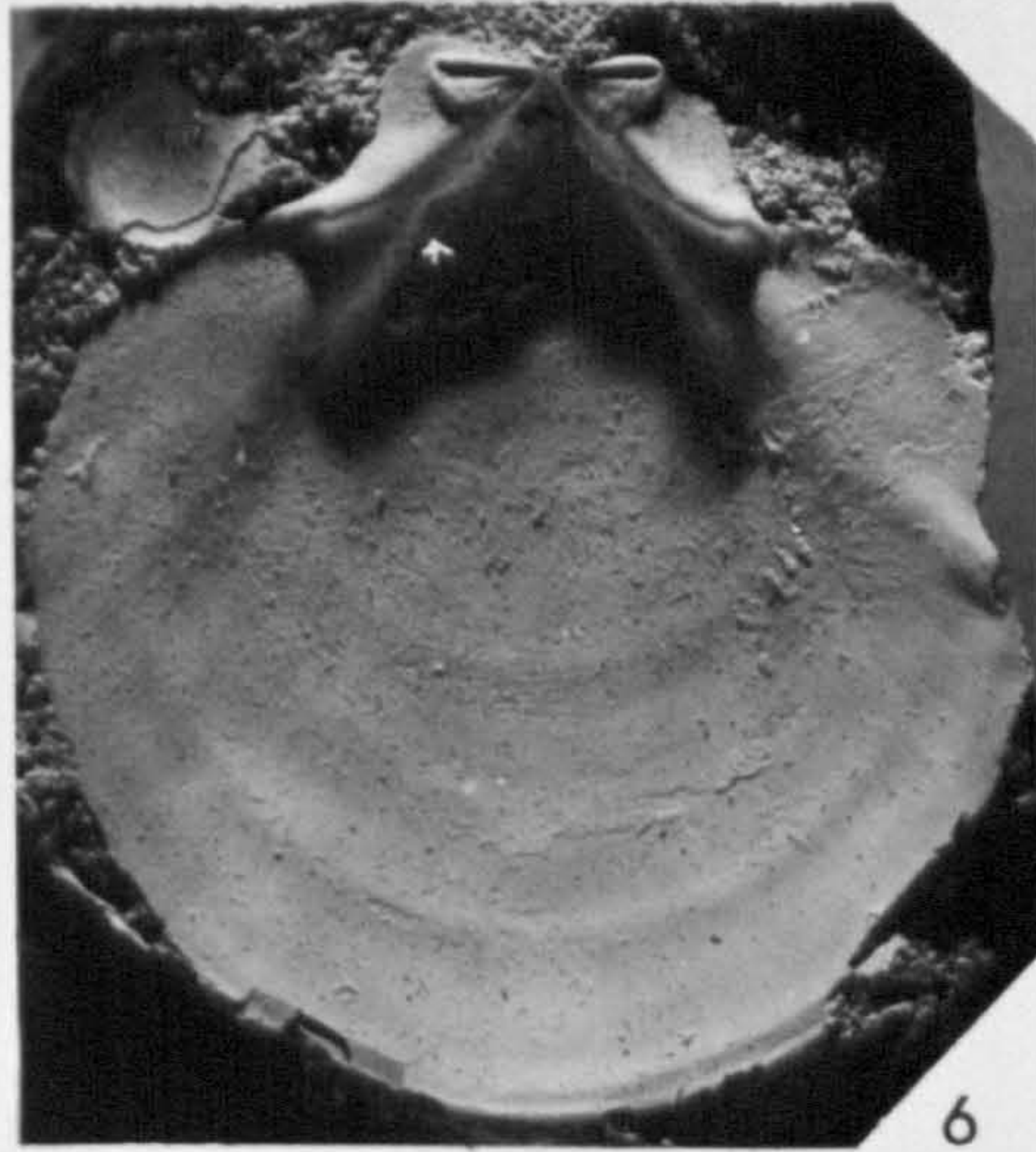
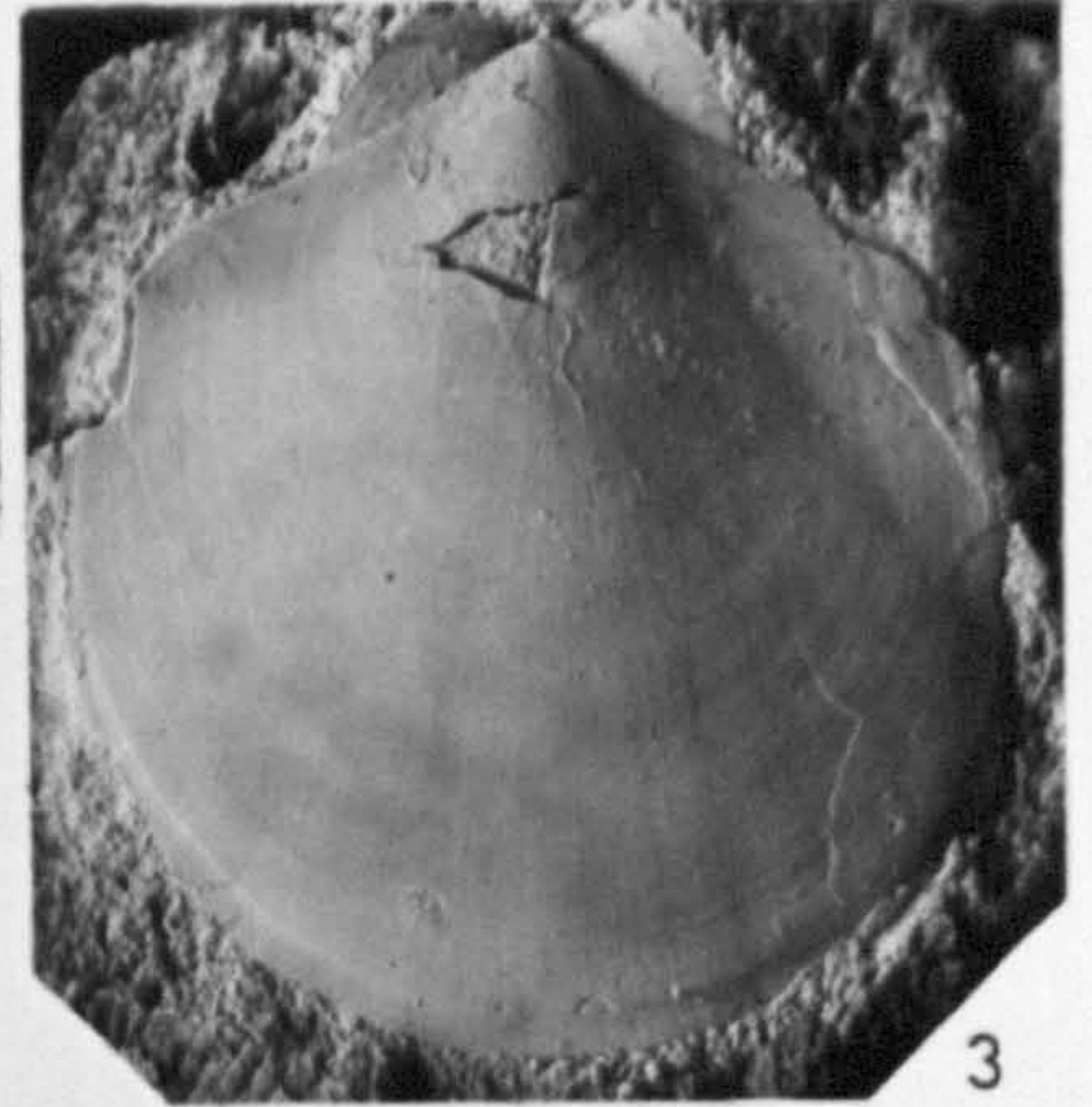
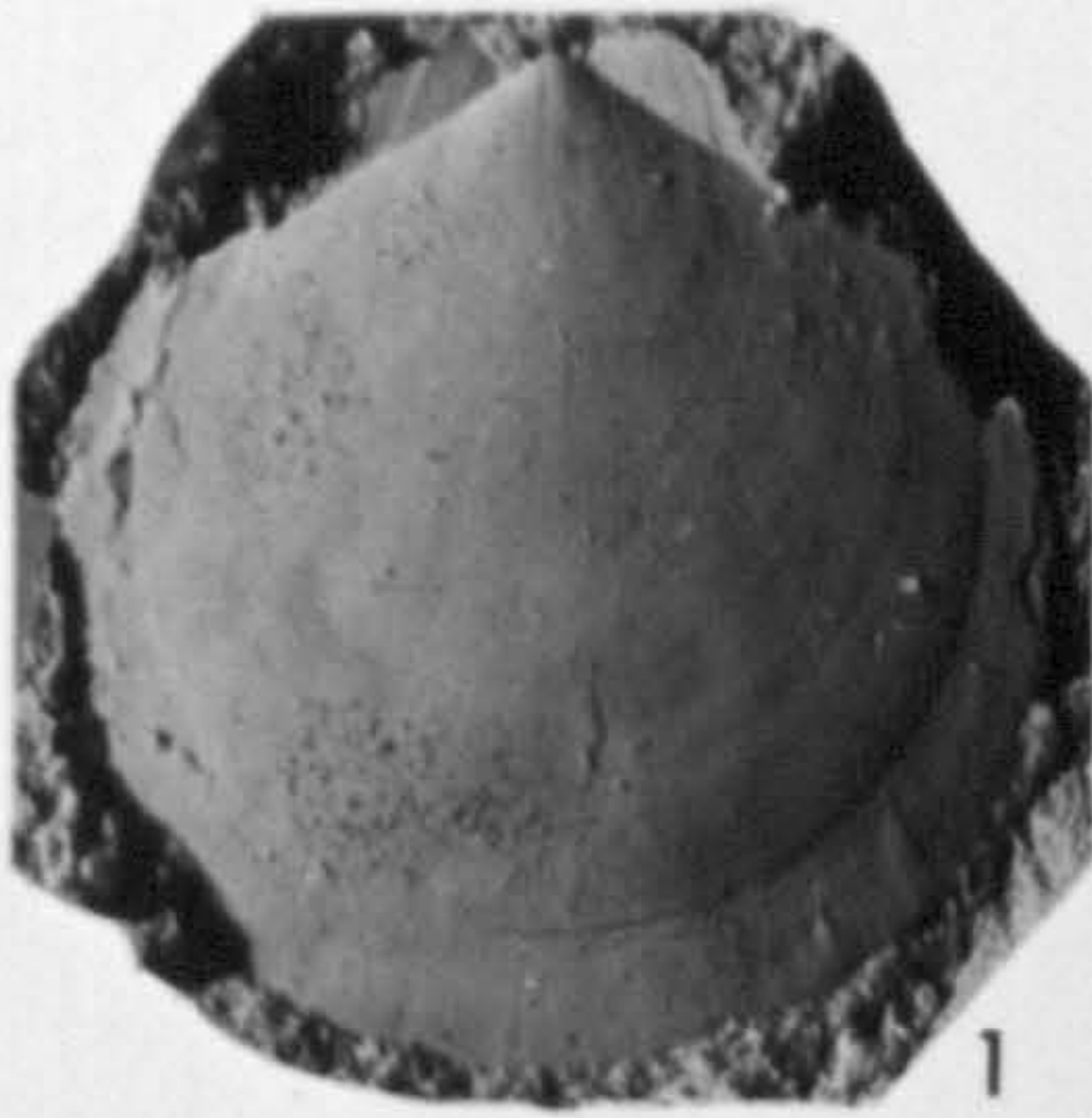
Fig. 14. Arctotis intermedia Bodylevsky. 14, SRAK IG.2101, left valve x3, erratic block of Lower Spilsby Sandstone, P. oppressus Zone, Middle Volgian Bawsey Warren, Norfolk.

PLATE 3



EXPLANATION OF PLATE 4

Figs. 1, 2, 3, 4, 5, 6, 7a, b, 8, 9a, b, 10a, b. Entolium (Entolium) orbiculare (J. Sowerby): 1, SRAK IG.2548, silicone rubber cast of left valve exterior; 3, IG.2518, left valve exterior; 7a, b, IG.2511, right valve interior, 7b x2, showing absence of resilifer; 8, IG.2527, silicone rubber cast of left valve exterior; 9a, b, IG.2501, silicone rubber cast of left valve interior, 9b x2, showing presence of resilifer; 10a, b, IG.2541, silicone rubber cast of right valve interior, 10b x2, showing presence of resilifer, Bed 1 calcareous concretions, Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, High Barn, West Keal, Lincs. 2, SRAK IG.1787, silicone rubber cast of right valve exterior showing commarginal grooves, Bed 6 calcareous concretions, Lower Spilsby Sandstone, S. lamplughii Zone, Upper Volgian, Nettleton, Lincs. 4, SRAK IG.594, immature right valve exterior; 5, IG.694, immature right valve exterior; earliest stages with commarginal grooves, latest part smooth, erratic boulders of Lower Spilsby Sandstone, P. oppressus Zone, Middle Volgian, Bawsey Warren, Norfolk. 6, IGS R27/O6, Rose Collection, right valve interior, probably Lower Spilsby Sandstone, $\frac{1}{2}$ mile north west of West Keal Church, Lincs.



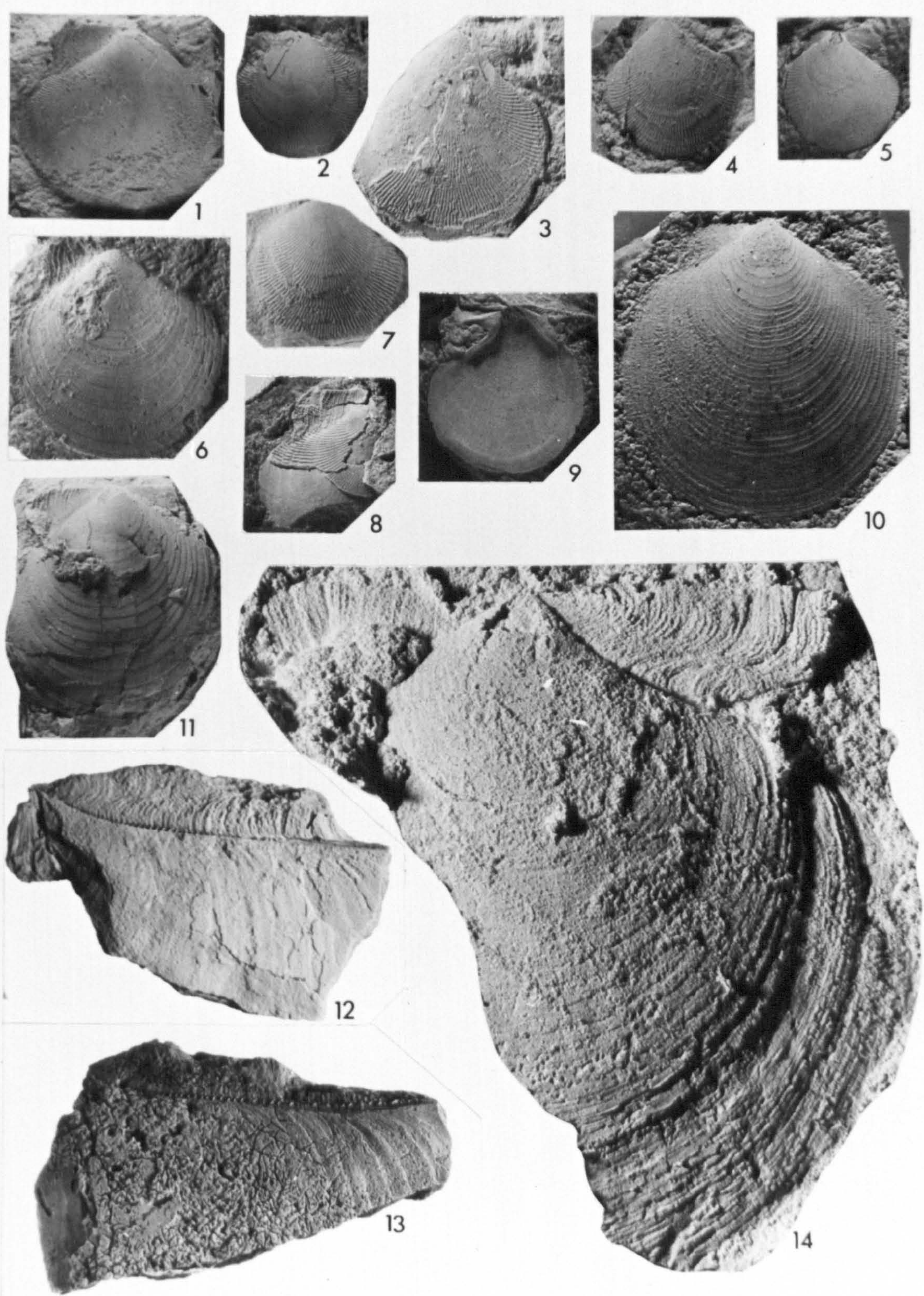
EXPLANATION OF PLATE 5

Figs. 1, 2, 3, 4, 5, 7, 8, 9. Camptonectes (Camptonectes) morini (de Lorient)

1, SRAK IG.2100, silicone rubber cast of left valve exterior, Bed 2, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs. 2, SRAK IG.1760, left valve exterior; 3, IG.579, right valve exterior; 4, IG.2099, silicone rubber cast of right valve exterior; 5, IG.692, right valve exterior (see also pl. 6, fig.3); 8, IG.483, left valve exterior; 9, IG.1739, right valve interior, erratic blocks of Lower Spilsby Sandstone, P. oppressus Zone, Middle Volgian, Bawsey Warren, Norfolk. 7, IGS CE 3406, left valve exterior (see also pl. 6, fig. 5), same horizon and locality.

Figs. 6, 10, 11, 12, 13, 14. Camptonectes (Boreionectes) cinctus (J.

Sowerby). 6, IGS CE 1563, silicone rubber cast of left valve exterior; 11, CE 5023, left valve exterior, Mintlyn Beds, H. kochi Zone, Ryazanian, West Dereham Flood Relief Channel, Norfolk. 10, IG. 1807, silicone rubber cast of left valve, Bed 6 calcareous concretion, Lower Spilsby Sandstone, Nettleton, Lincs. 12, SRAK JG.660, fragment of right valve exterior surface, showing ctenolium stopping short of the byssal notch, Claxby Ironstone, unhorizoned, Nettleton, Lincs. 13, KY570, lower Tealby Beds unhorizoned, Nettleton, Lincs. 14, JG.421, silicone rubber cast of right valve, Upper Spilsby Sandstone, S. stenomphalus Zone, Ryazanian, Moses Farm, Stenigot, Lincs.

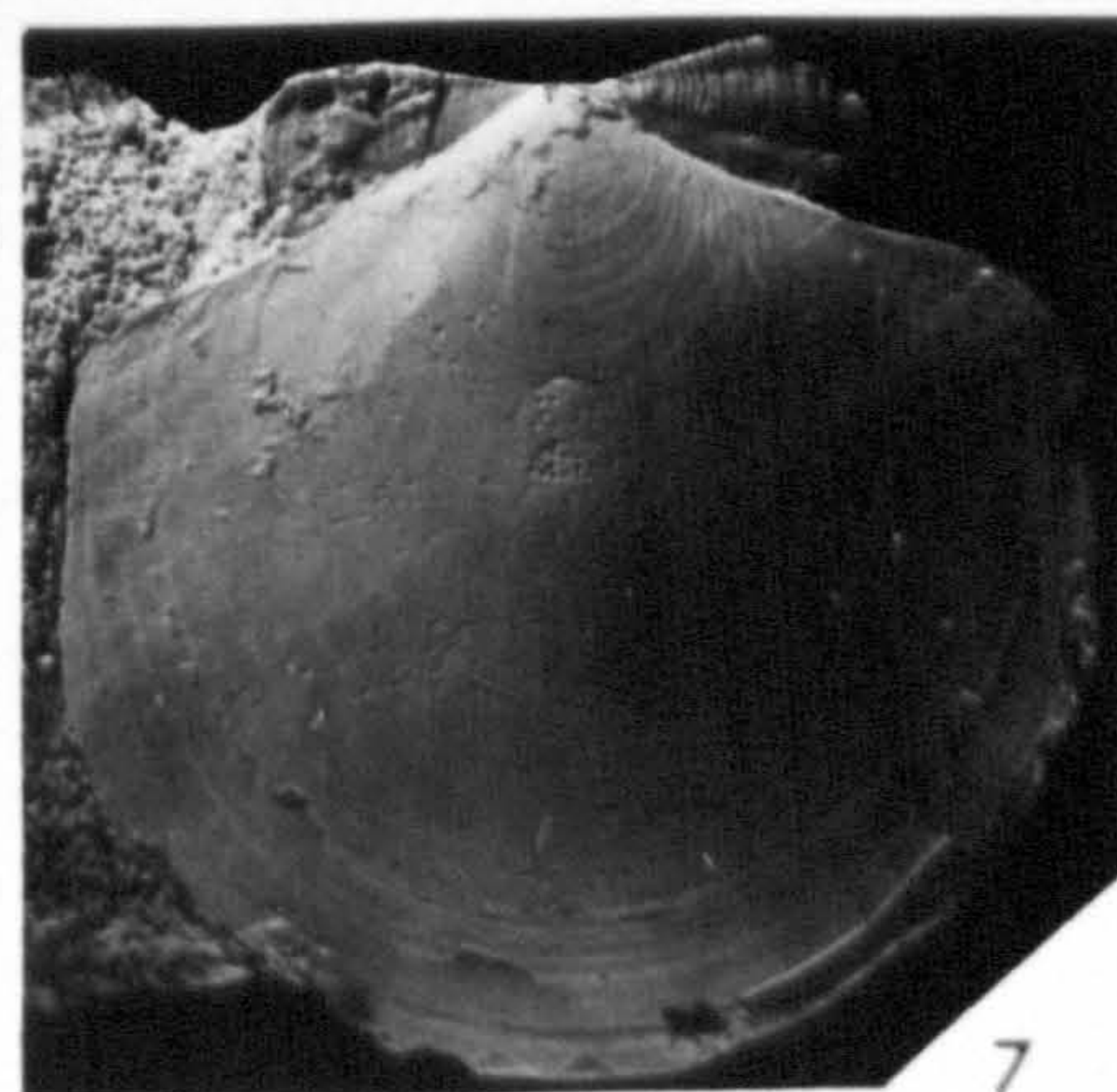
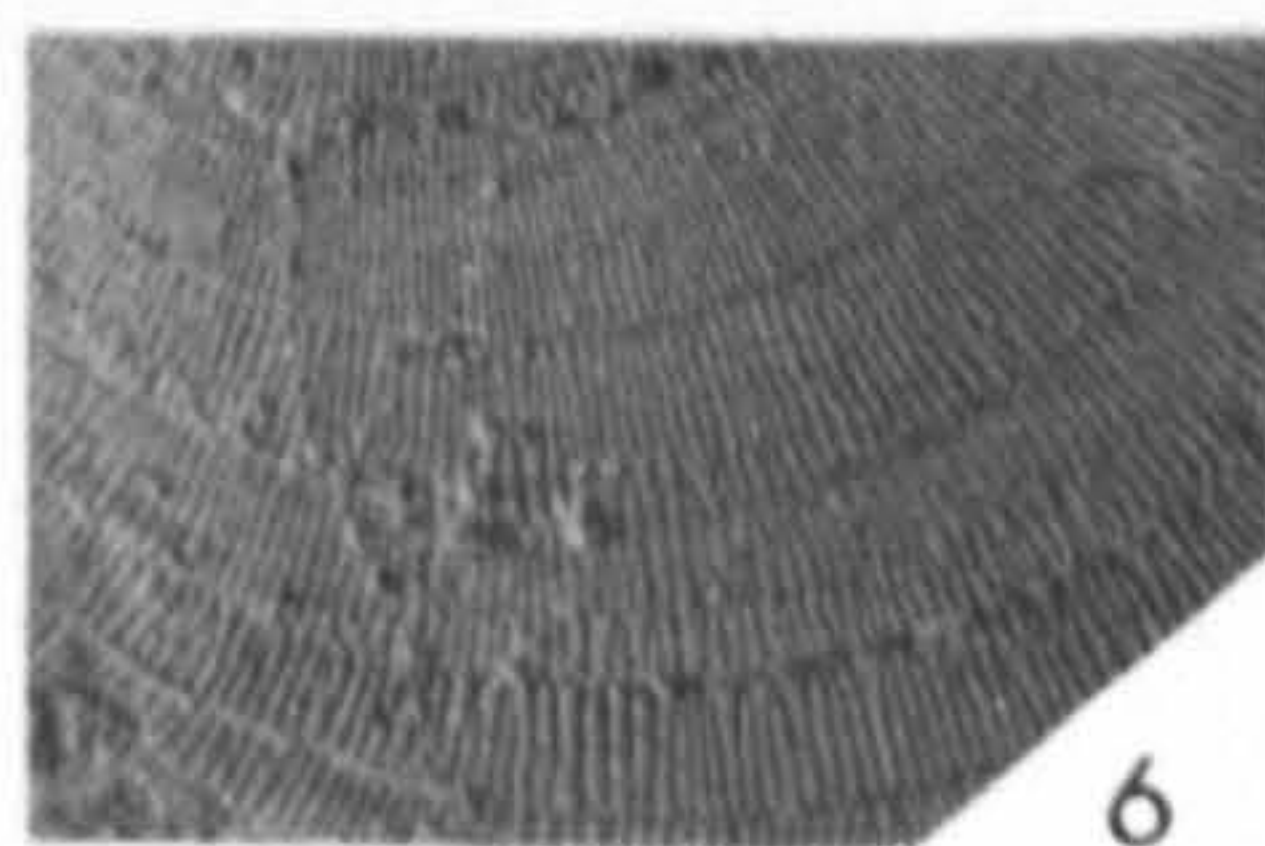
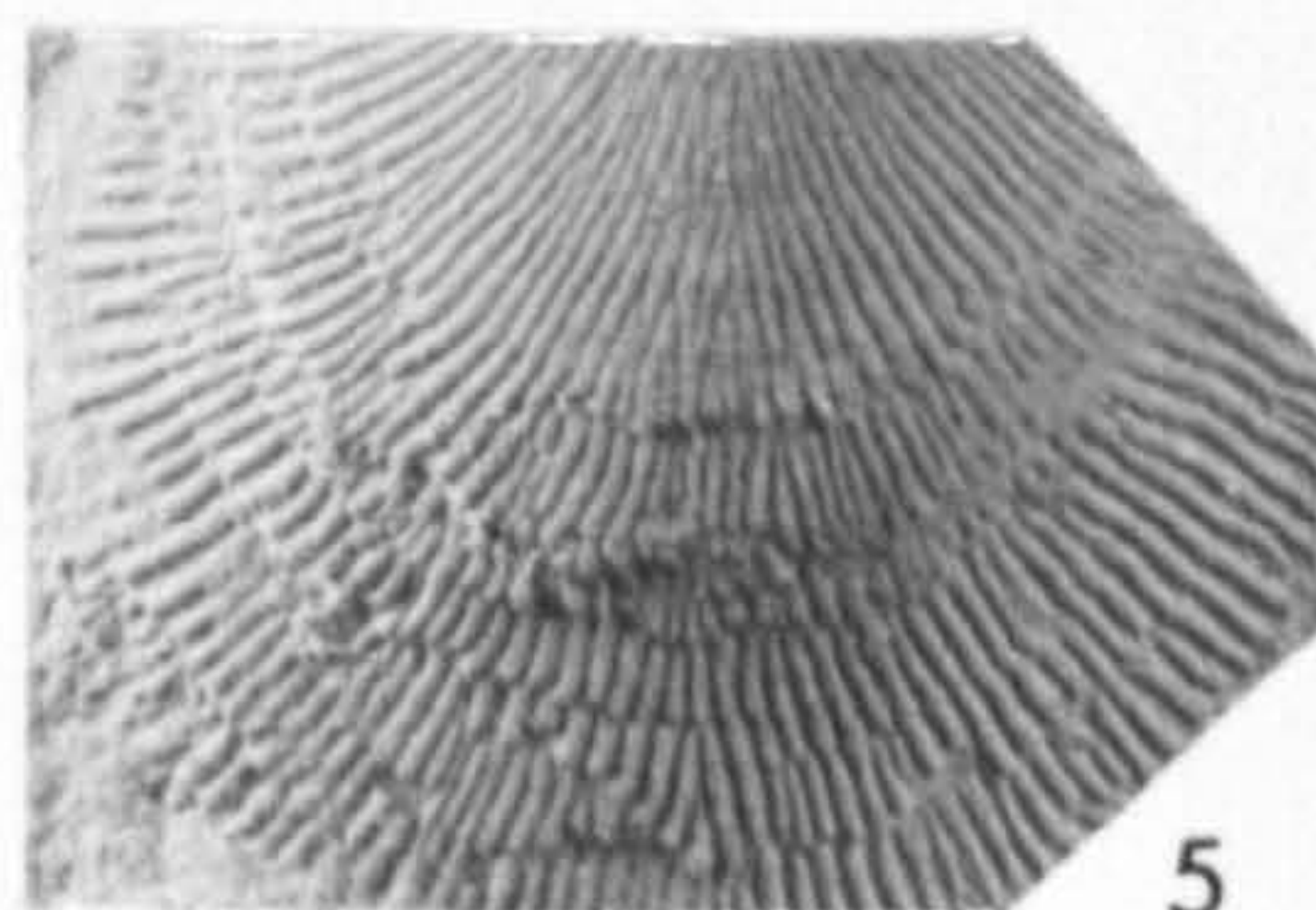
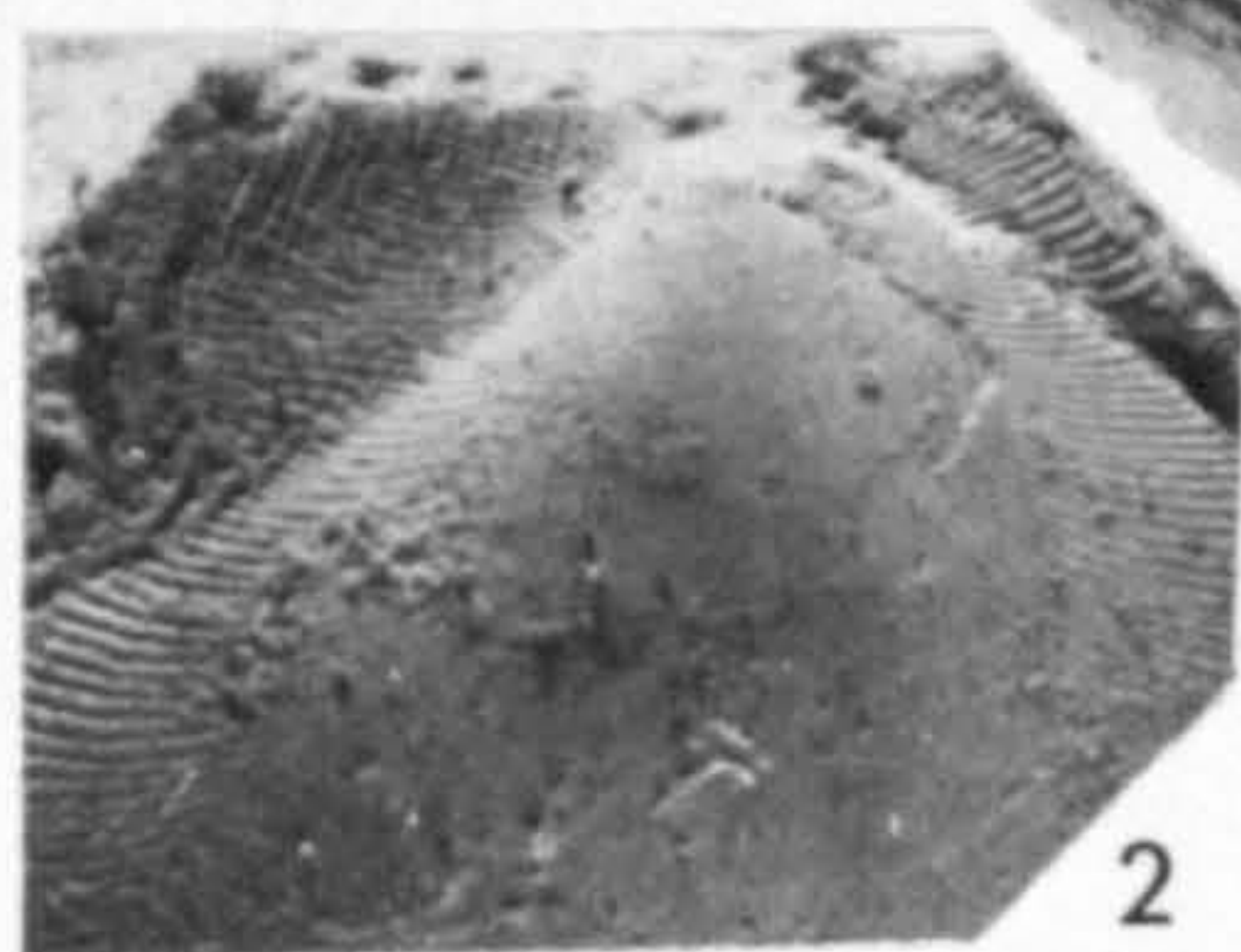
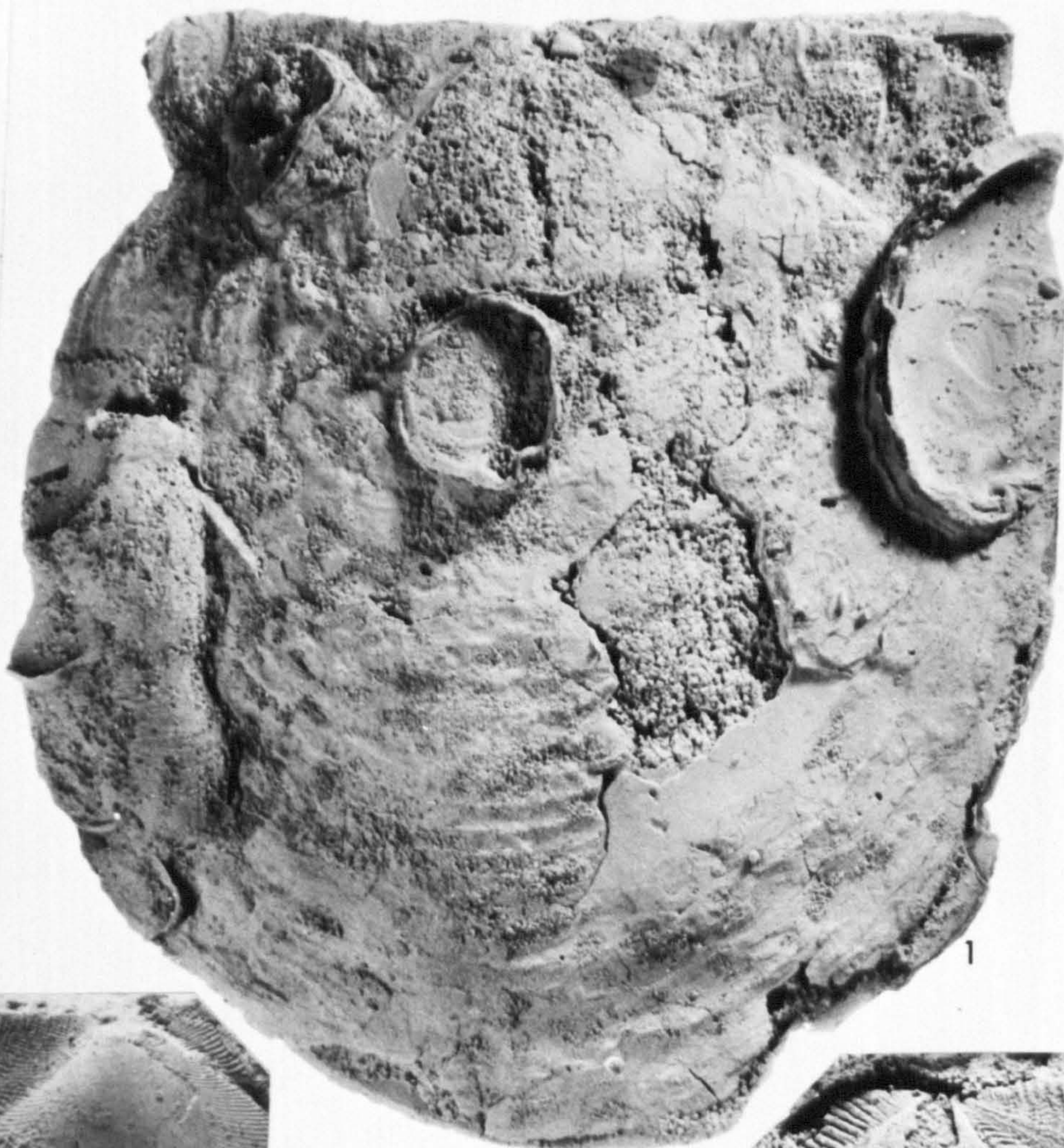


EXPLANATION OF PLATE 6

Figs. 1, 4, 6, 7. Camptonectes (Boreionectes) cinctus (J. Sowerby).

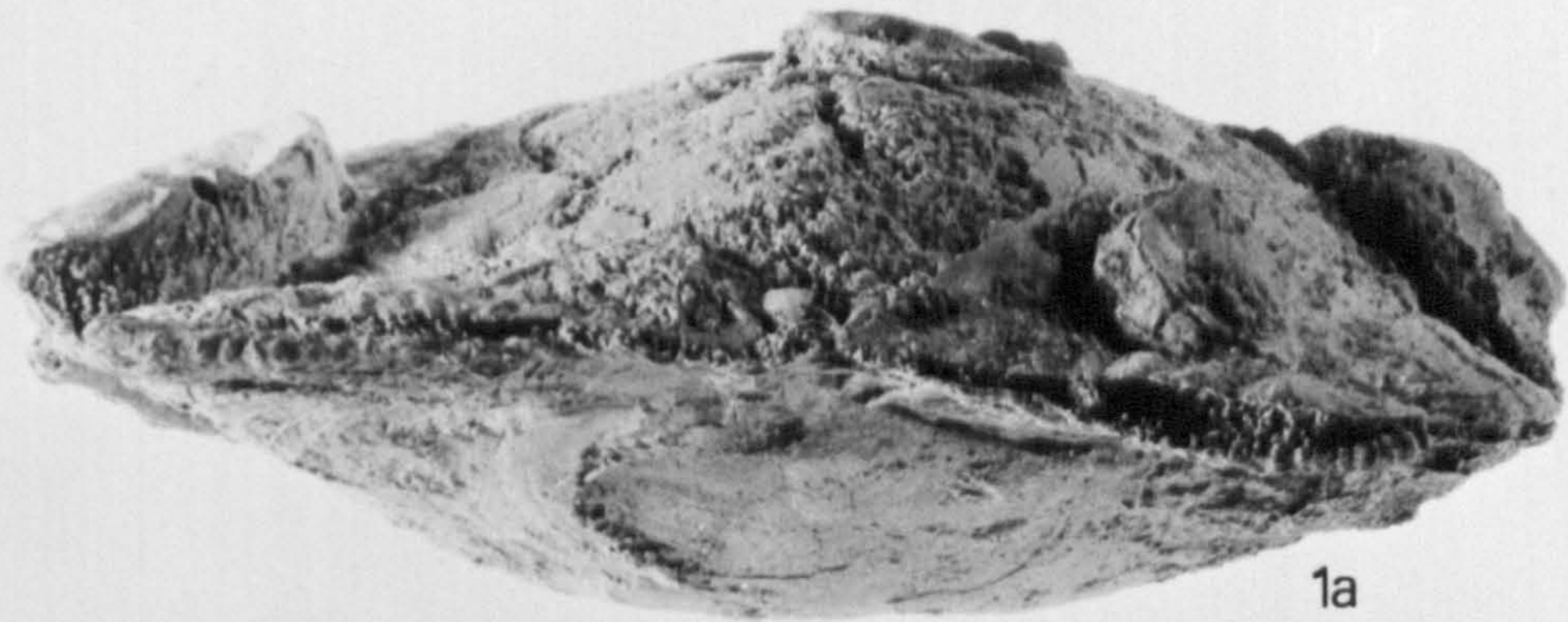
1, IGS Swinnerton Collection, TNN 255, (see also Plate 7, figs. 1a, b), left valve with adhering ostreids, probably Upper Spilsby Sandstone (fide Casey), Fordington Borehole, Lincs. 4, SRAK IG.423, silicone rubber cast of left valve, anterior auricle, Upper Spilsby Sandstone, S. stenomphalus Zone, Ryazanian, Moses Farm, Stenigot, Lincs. 6, IGS CE1583 (see also Plate 5, fig. 6) silicone rubber cast of left valve, enlarged x2, showing detail of exterior ornament, Mintlyn Beds, H. kochi Zone, Ryazanian, West Dereham Flood Relief Channel, Norfolk. 7, PFR 247, right valve showing ctenolium spines projecting in byssal notch, reduced x 0.9, upper part of Claxby Ironstone, Upper Valanginian/Hauterivian, Nettleton, Lincs.

Figs. 2, 3, 5. Camptonectes (Camptonectes) morini (de Loriol). 2, SRAK IG.2100, (see also Plate 5, fig. 1), silicone rubber cast of left valve exterior auricular region, enlarged x2, Bed 2, Basal Spilsby Nodule Bed, Nettleton, Lincs. 3, IG.692 (see also Plate 5, fig. 5), right valve, exterior auricular region, enlarged, x2, erratic block of Lower Spilsby Sandstone, P. oppressus Zone, Middle Volgian, Leziate, Norfolk. 5, IGS CE 3406 (see also Plate 5, figure 7), detail of surface ornament, enlarged, x2, same horizon and locality as fig. 3.

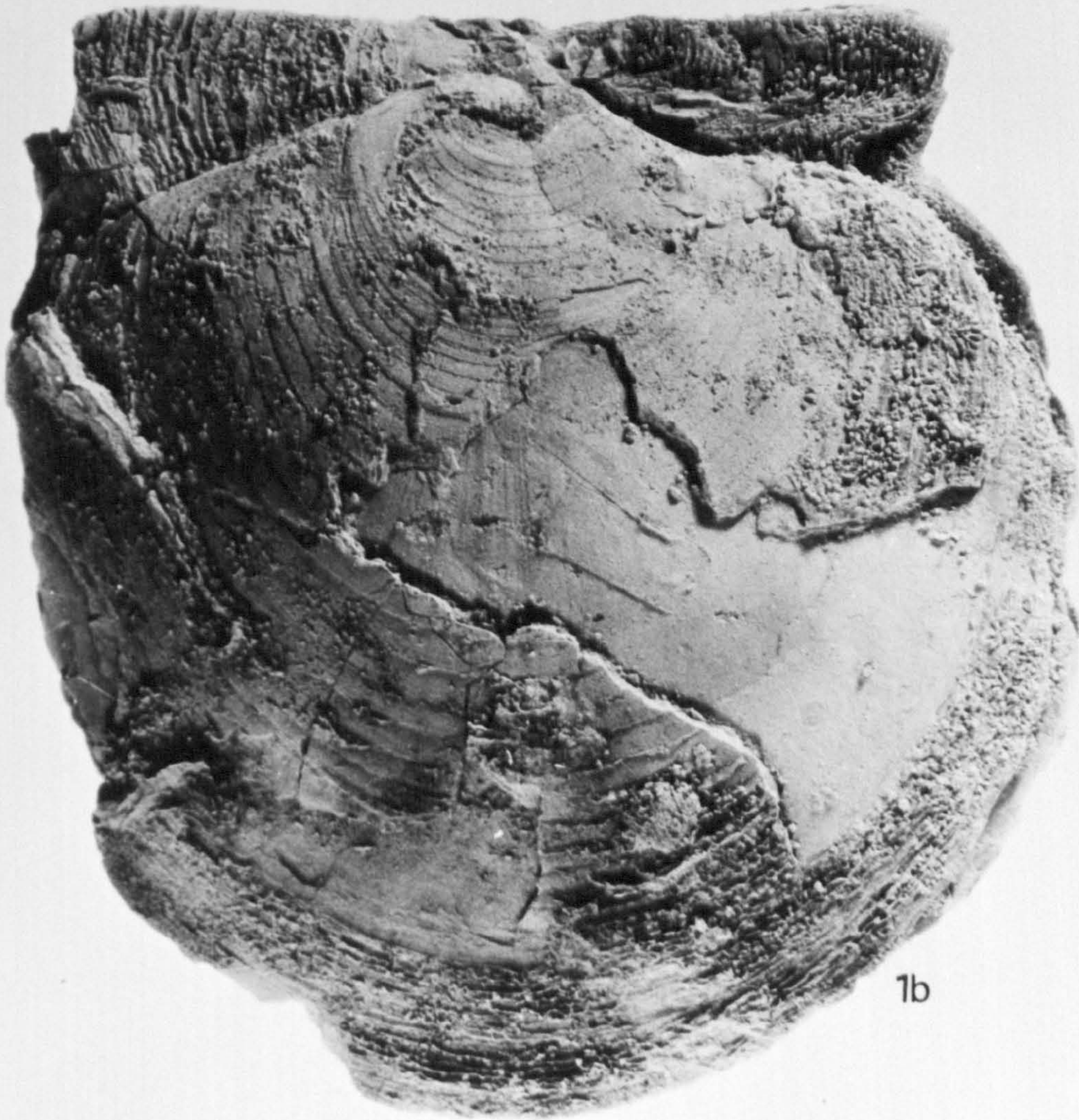


EXPLANATION OF PLATE 7

Figs. 1a, b. Camptonectes (Boreionectes) cinctus (J. Sowerby). IGS Swinnerton Collection, TMN 255, 1a, dorsal aspect; 1b, right lateral aspect (see also Plate 6, fig. 1), Upper Spilsby Sandstone (fide Casey), Fordington Borehole, Lincs.



1a



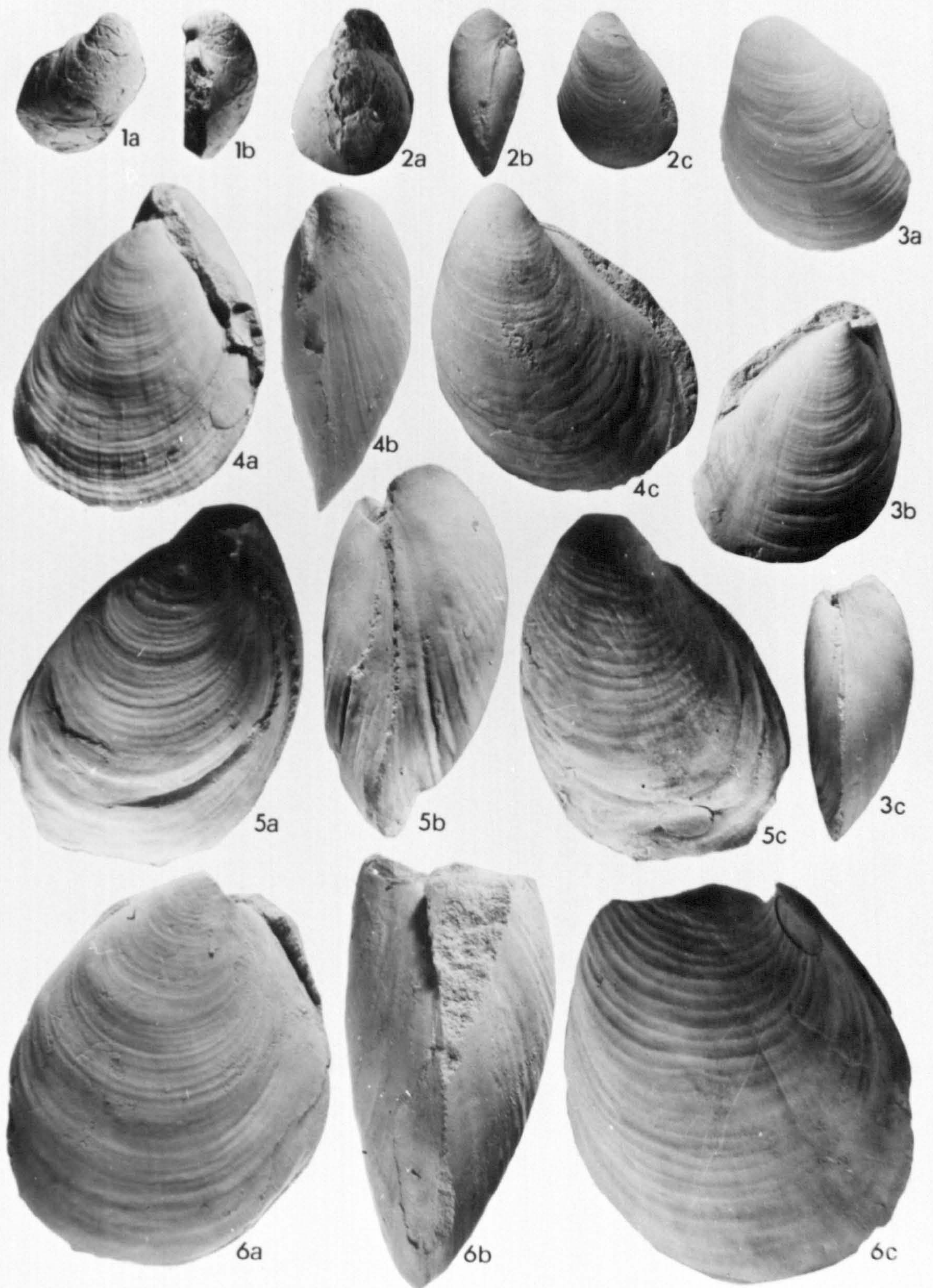
1b

EXPLANATION OF PLATE 8

Figs. 1a, b. Buchia rugosa (Fischer de Waldheim). SRAK IG.1382, phosphatised internal mould of right valve, Basal Spilsby Nodule Bed, Middle Volgian, Mettleton, Lincs.

Figs 2a-c, 3a-c, 4a-c, 5a-c, 6a-c. Buchia volgensis (Lahusen). 2a-c, SMC B.11239, steinkern; 4a-c, B.11338, steinkern, originally figured as type of Aucella volgensis var radiolata ssp. nov. Pavlow 1896, pl. 27, fig. 2; 5a-c, B.11337, steinkern, originally figured as Aucella volgensis Lahusen by Pavlow, 1896, pl. 27, fig. 1; Spilsby Sandstone, unhorizoned but believed by Casey (1973, p. 204) to be from the S. stenomphalus Zone, Ryazanian, Donnington, Lincs. 3a-c, BMNH 81075, steinkern; 6a-c, BMNH 81069, steinkern, labelled Birken Haven, but probably the same horizon and locality as figs. 2, 4 and 5.

PLATE 8

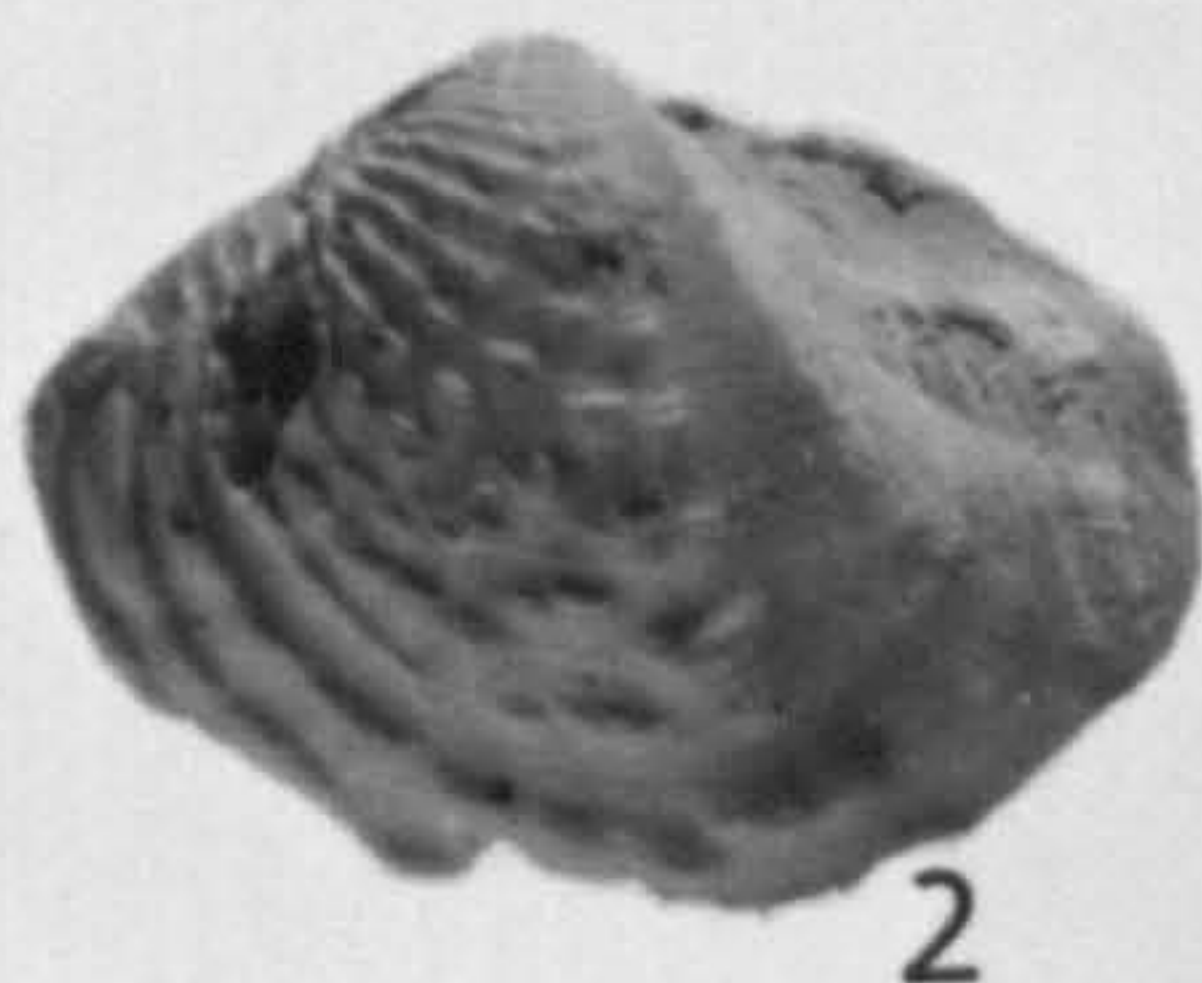
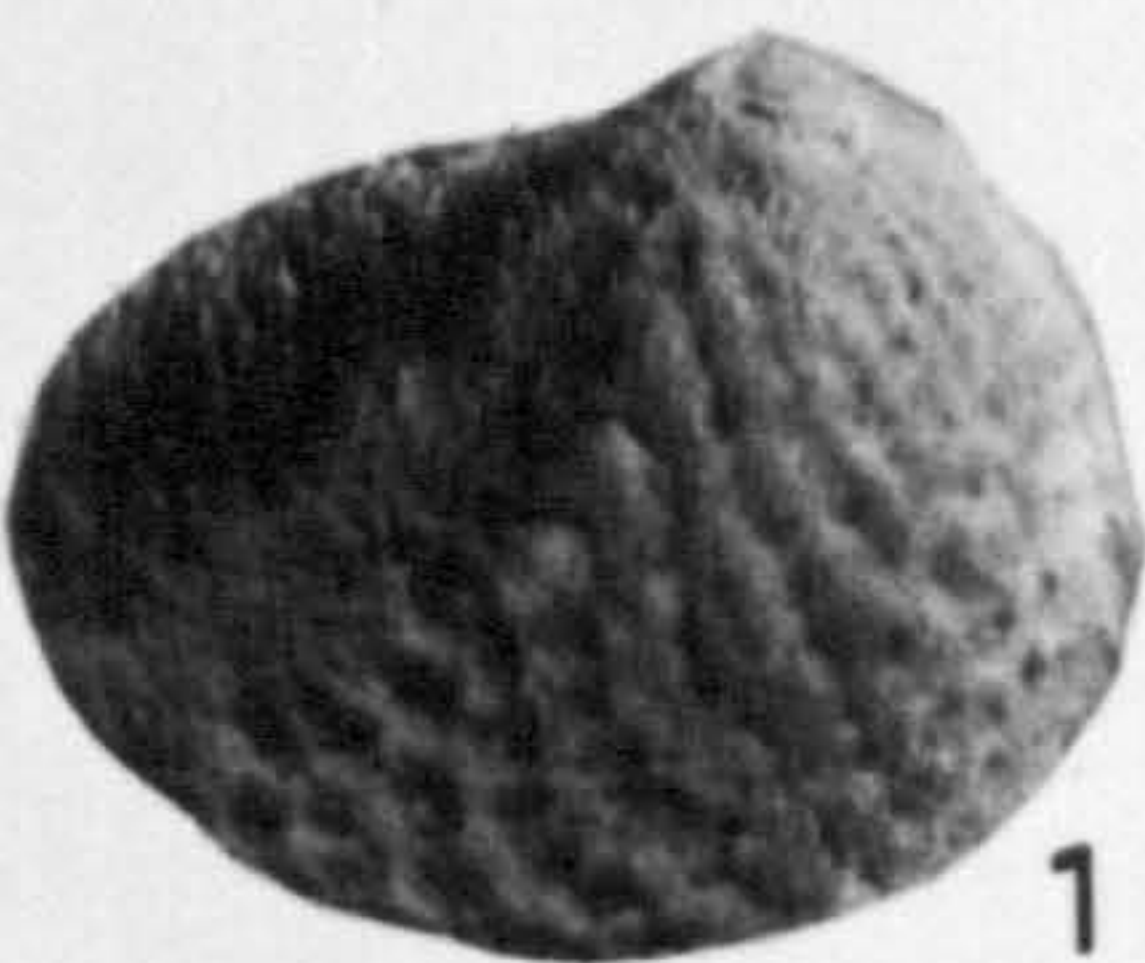


EXPLANATION OF PLATE 9

Fig. 1. Laevitrignia (Laevitrignia) nanseli (Lycett). IGS CE 3752
silicone rubber cast of right valve, erratic block of Spilsby
Sandstone (?), Leziate, Norfolk.

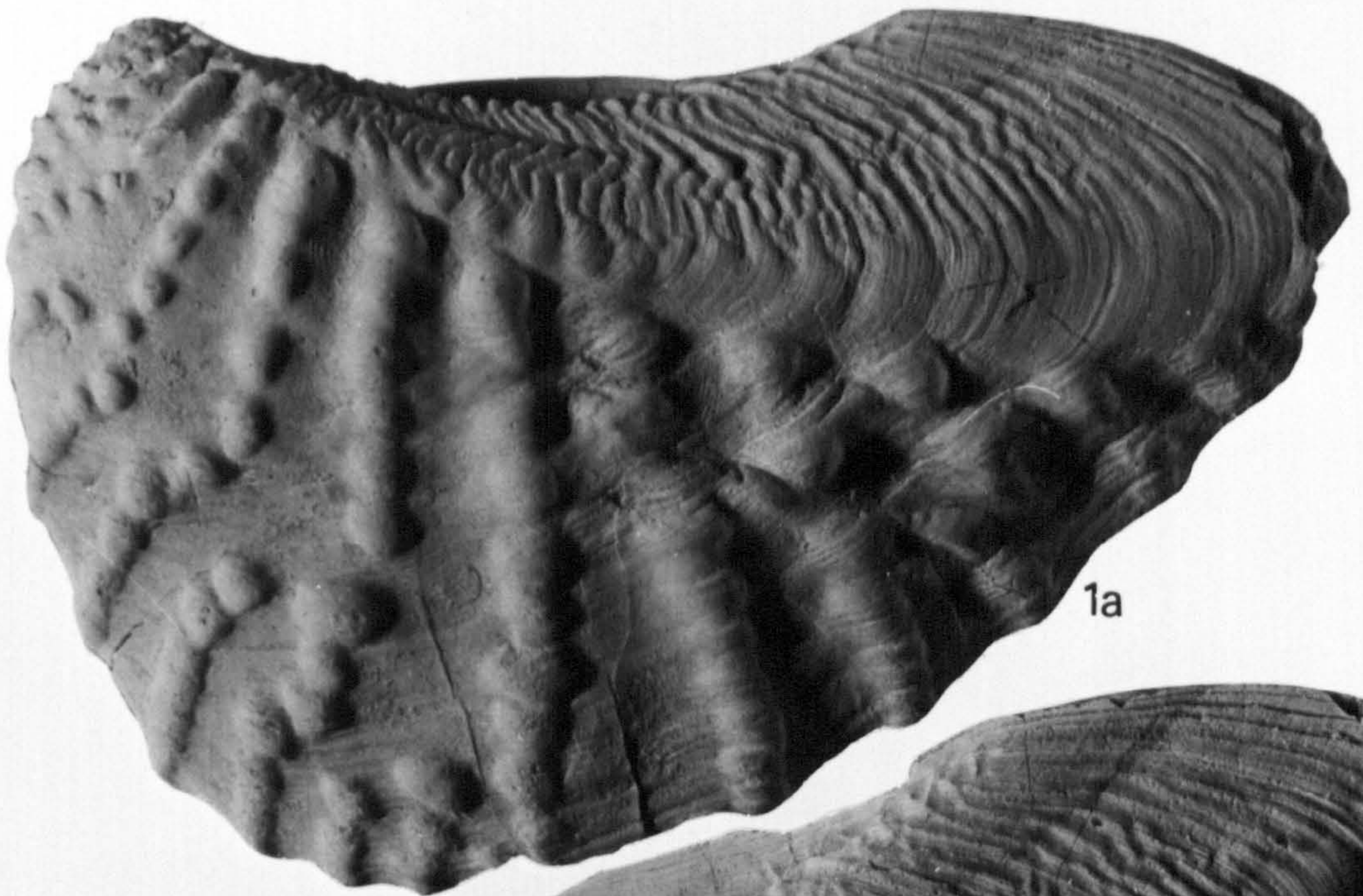
Fig. 2. Laevitrignia (Laevitrignia) wightensis (Strand). SMC
B.85668, left valve, reworked from Portland or Purbeck Beds (?),
presumed base of Lower Greensand, Potton, Beds.

Figs. 3a-c, 4a, b. Myophorella (Myophorella) intermedia (Fahrenkohl).
3a, b, SRAK IG.2498 (see also Plate 12, figure 2), silicone rubber
cast of right valve; 4a, b, IG.2498, silicone rubber cast of right
valve showing irregular anterior flank ornament, Bed 1 concretions,
Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian,
High Barn, West Keal, Lincs.



EXPLANATION OF PLATE 10

Figs. 1a-c, 2. Myophorella (Myophorella) intermedia (Fahrenkohl).
1a-c, BMNH 49987, (type of Trigonia exaltata Lycett, 1877, pl. 38, fig. 2), coarsely tuberculate left valve, labelled 'Neocomian Formation', presumably Sandringham Sands or an erratic block, from Downham, Norfolk; 2, SRAK IG.547, silicone rubber cast of posterior area of right valve, erratic block of Lower Spilsby Sandstone, P. oppressus Zone, Middle Volgian, Leziate, Norfolk.



EXPLANATION OF PLATE 11

Figs. 1a-c, 2a-c. Myophorella (Myophorella) intermedia (Fahrenkohl).
1a-c, GRAK IG.2499, silicone rubber cast of right valve; 2a-c,
silicone rubber cast of right valve, Bed 1 calcareous concretions,
Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian,
High Barn, West Keal, Lincs.

PLATE 11



1a



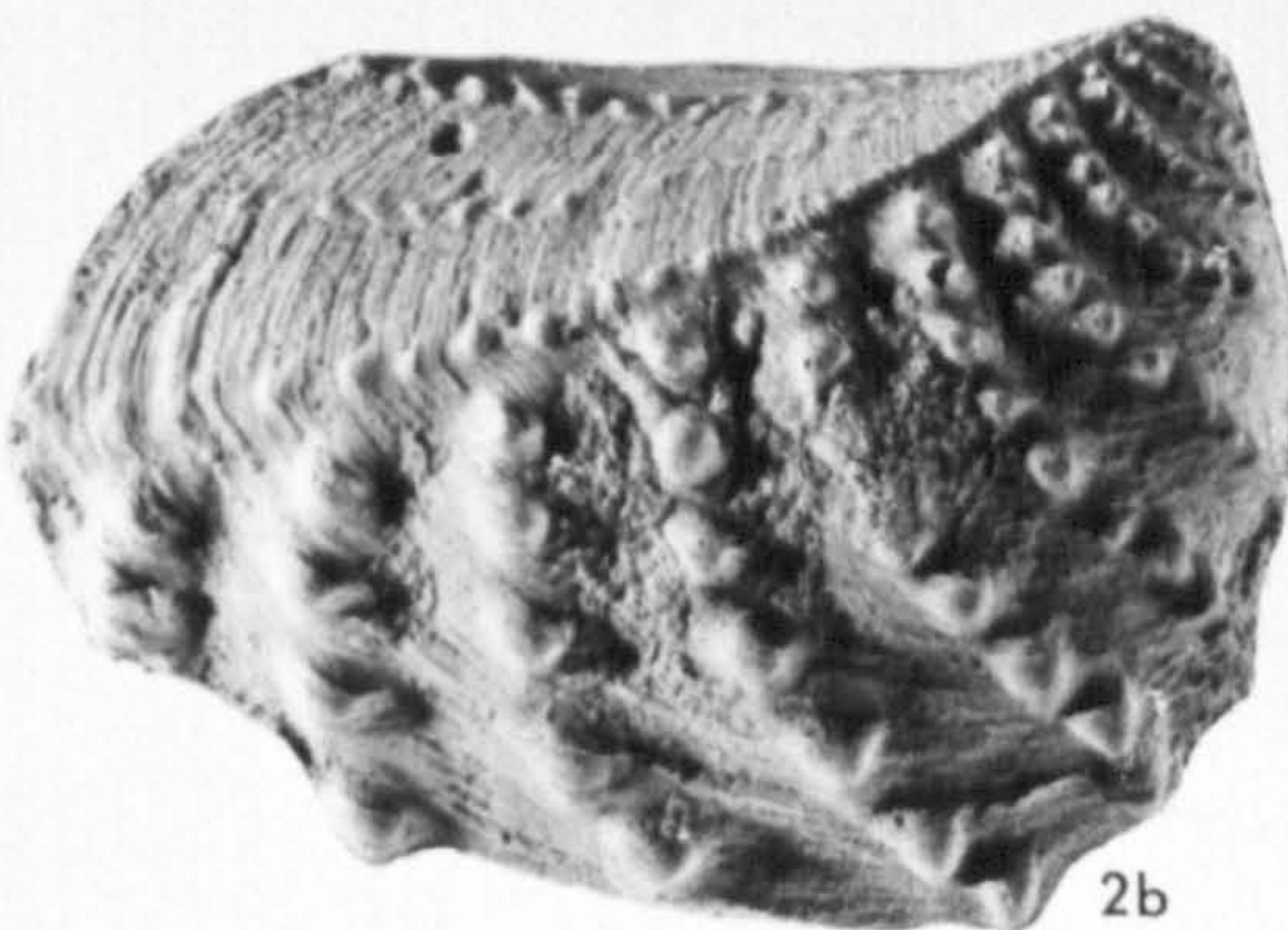
1b



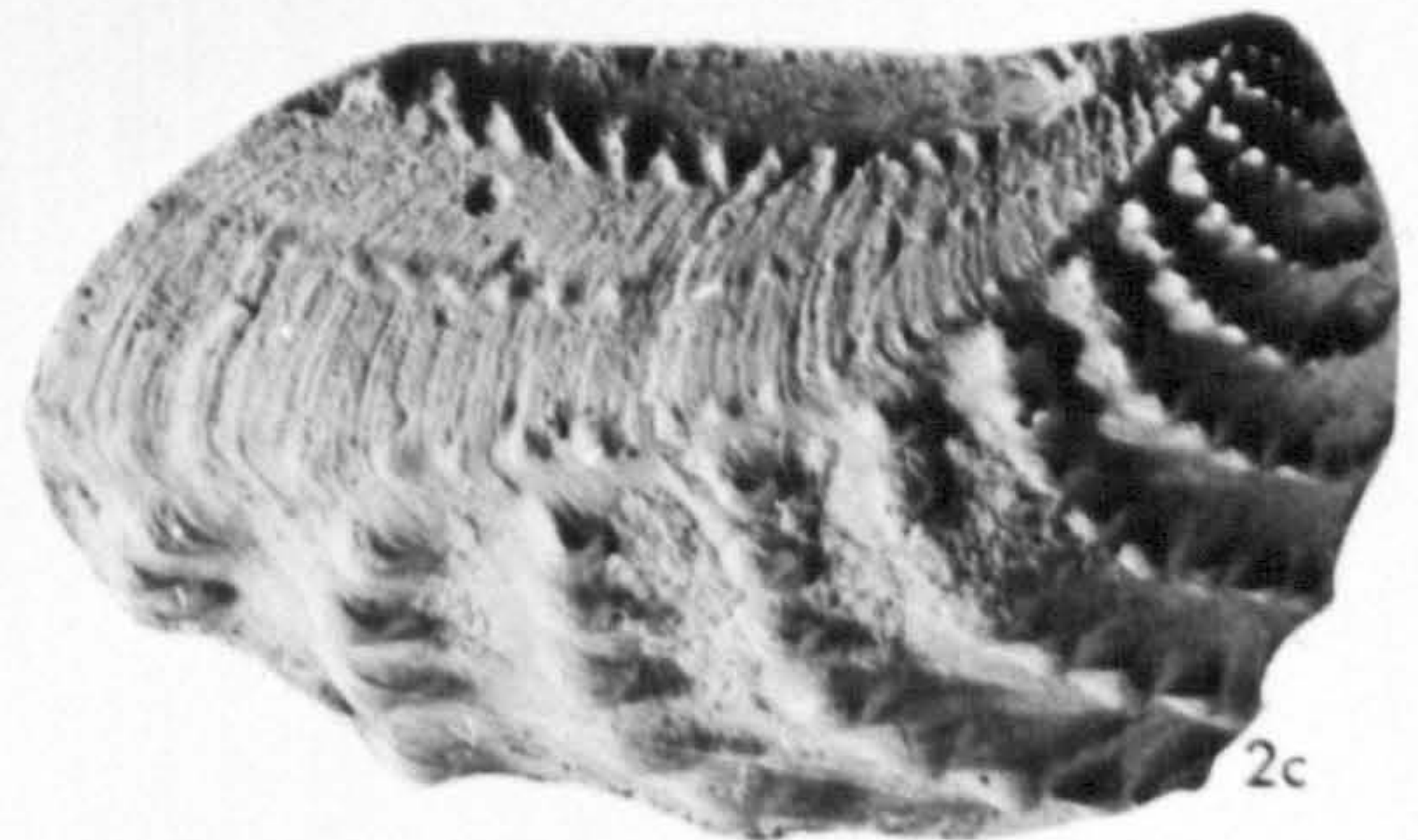
1c



2a



2b

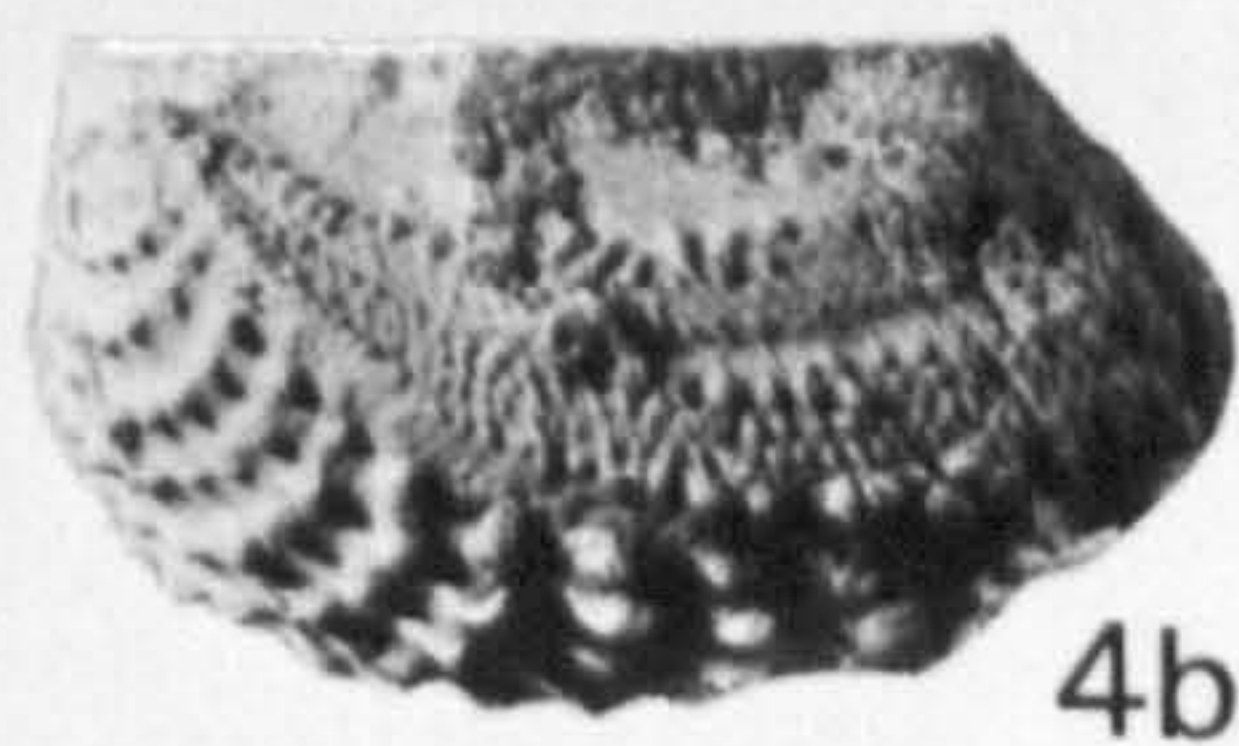
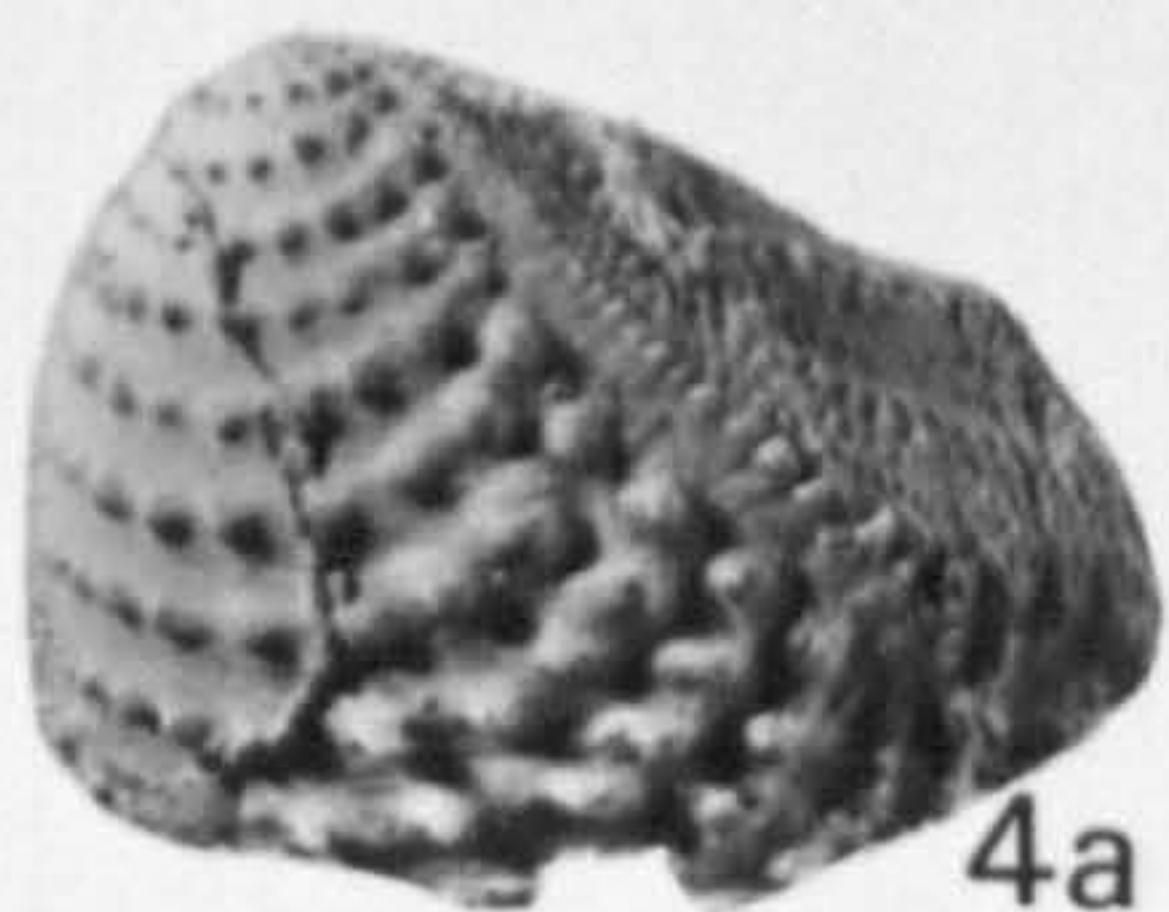
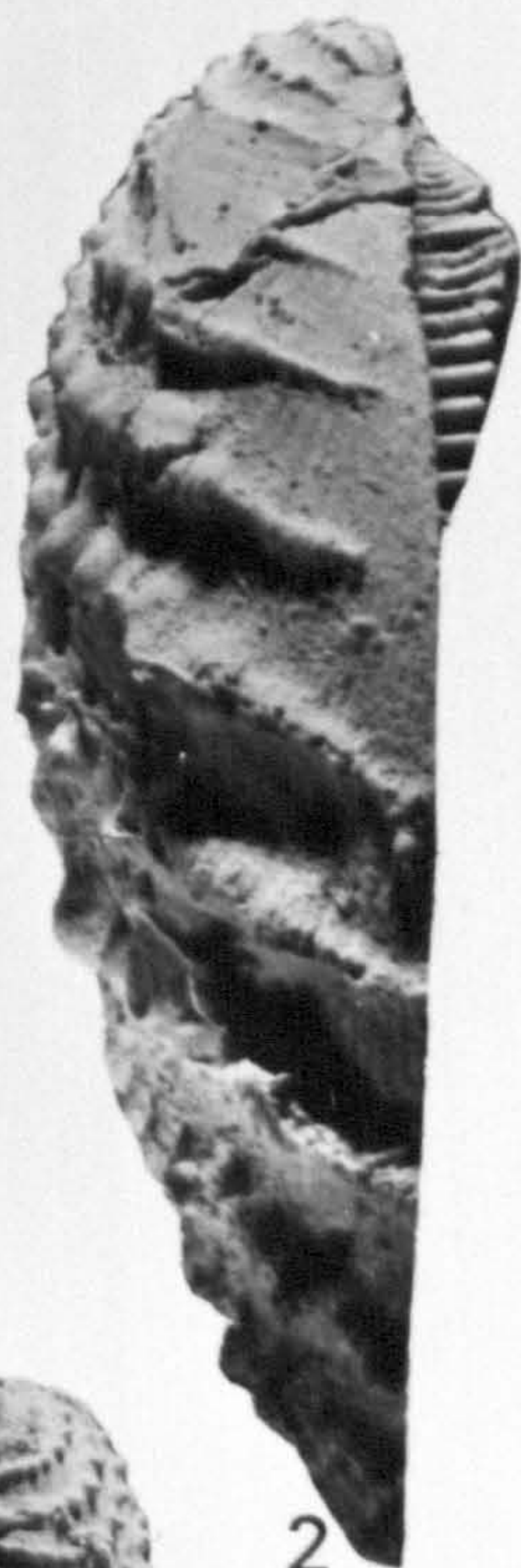


2c

EXPLANATION OF PLATE 12

Figs. 1, 2. Myophorella (Myophorella) intermedia (Fahrenkohl). Fig. 1, SRAX IG.2-96, silicone rubber cast of right valve; Fig. 2, IG.2498, silicone rubber cast of right valve, anterior view (see also Plate 9, figs. 3a-c), Bed 1 calcareous concretions, Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, High Barn, West Keal, Lincs.

Figs. 3, 4a-c. Myophorella (Myophorella) keepingi (Lycett). 3, IGS CE 4803, silicone rubber cast of incomplete right valve, Bed 10, Mintlyn Beds, S. stenomphalus Zone, Ryazanian, Mintlyn Wood, Norfolk. 4a-c, SRAX JG.418, silicone rubber cast of left valve, Mid Spilsby Nodule Bed, unphosphatised, S. icenii Zone, Ryazanian, Winceby Rectory, Lincs.



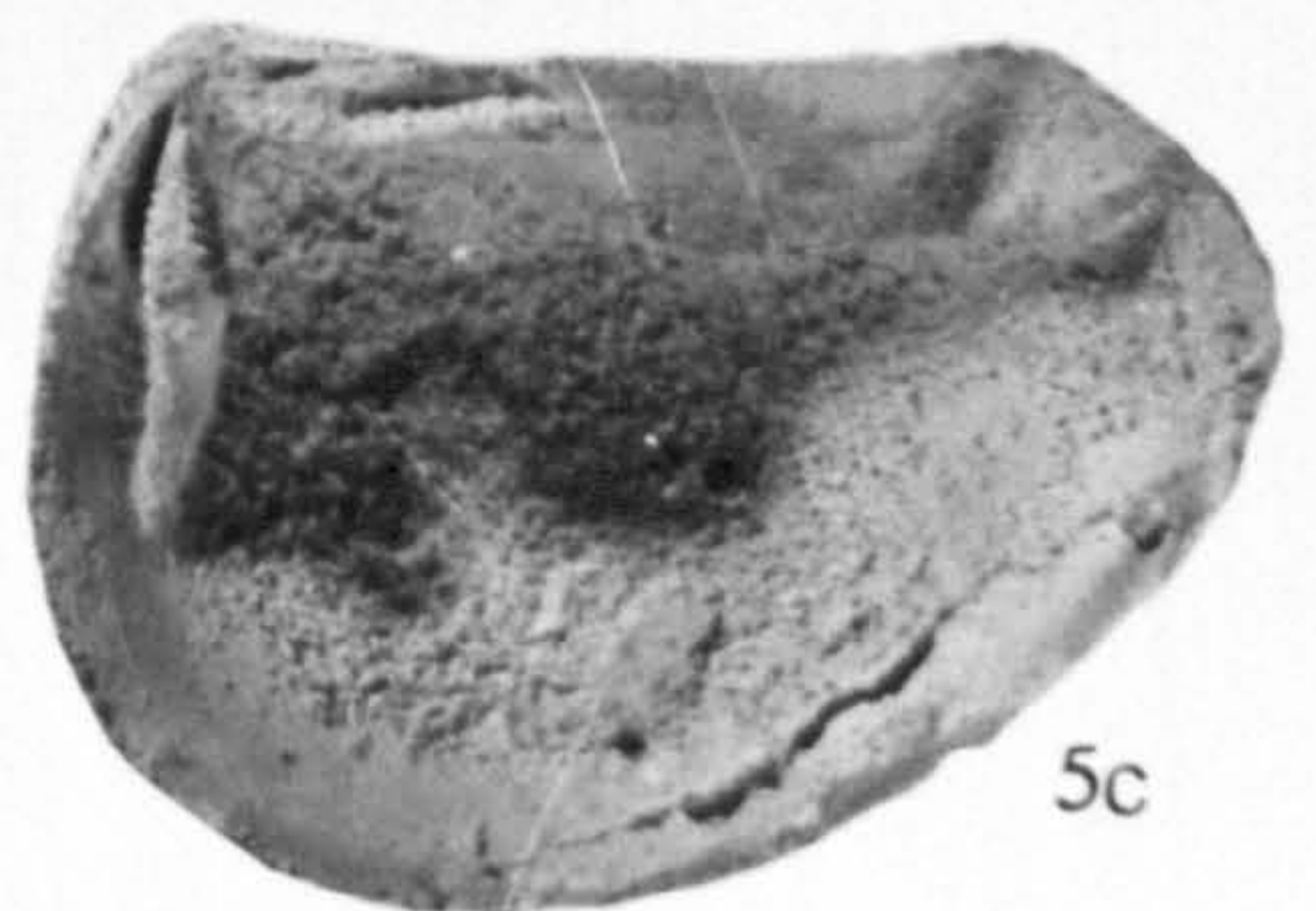
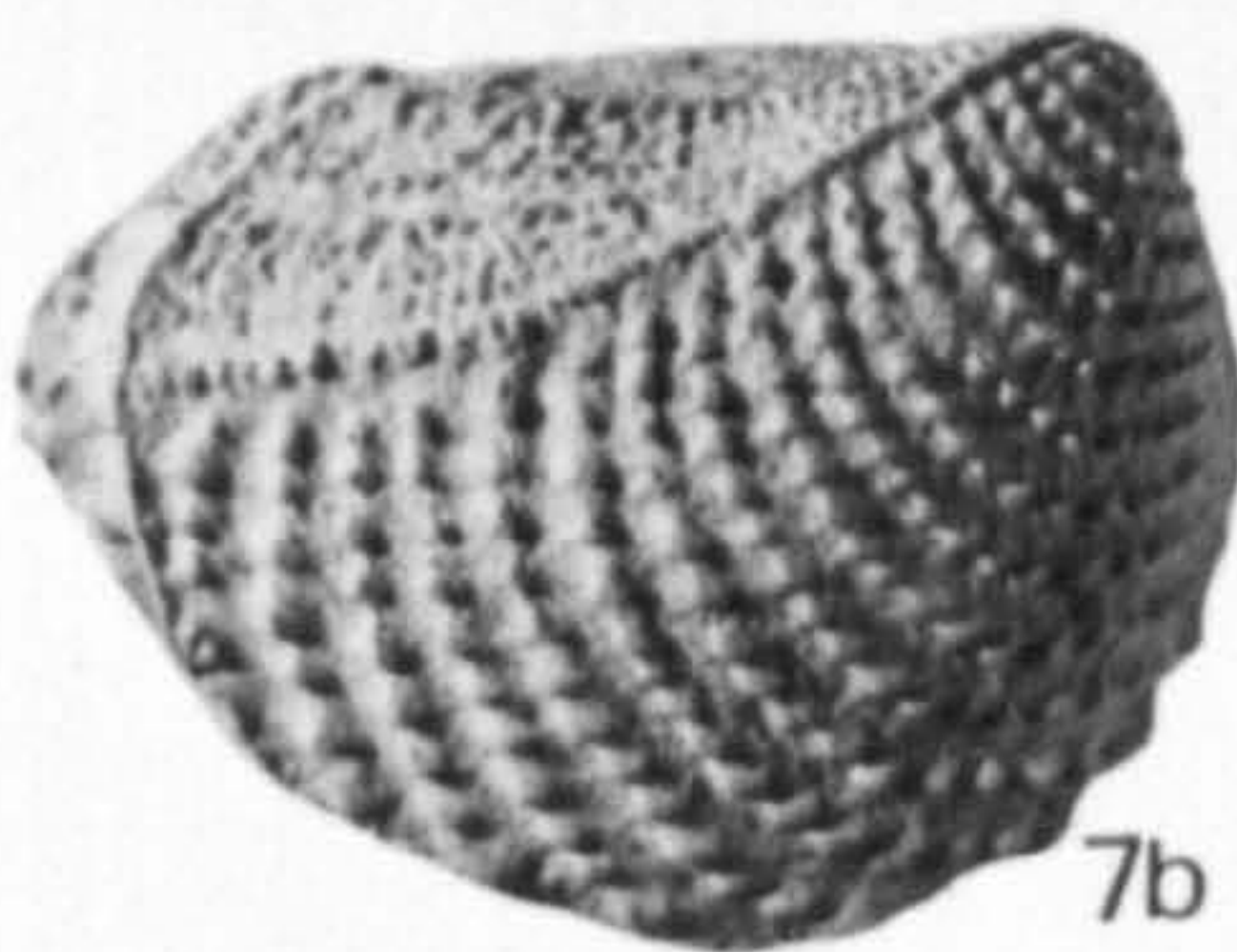
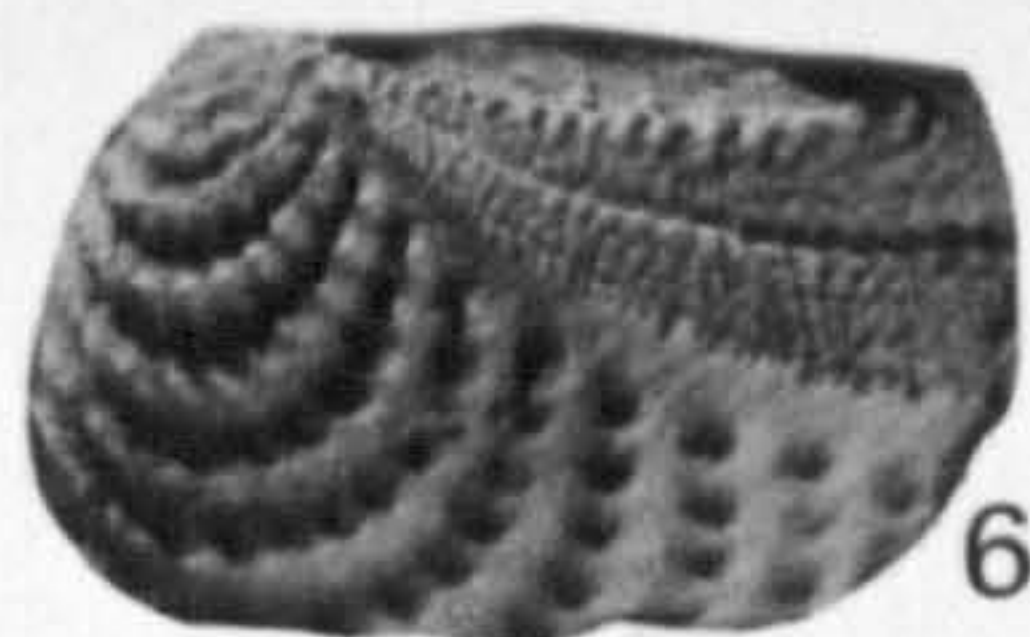
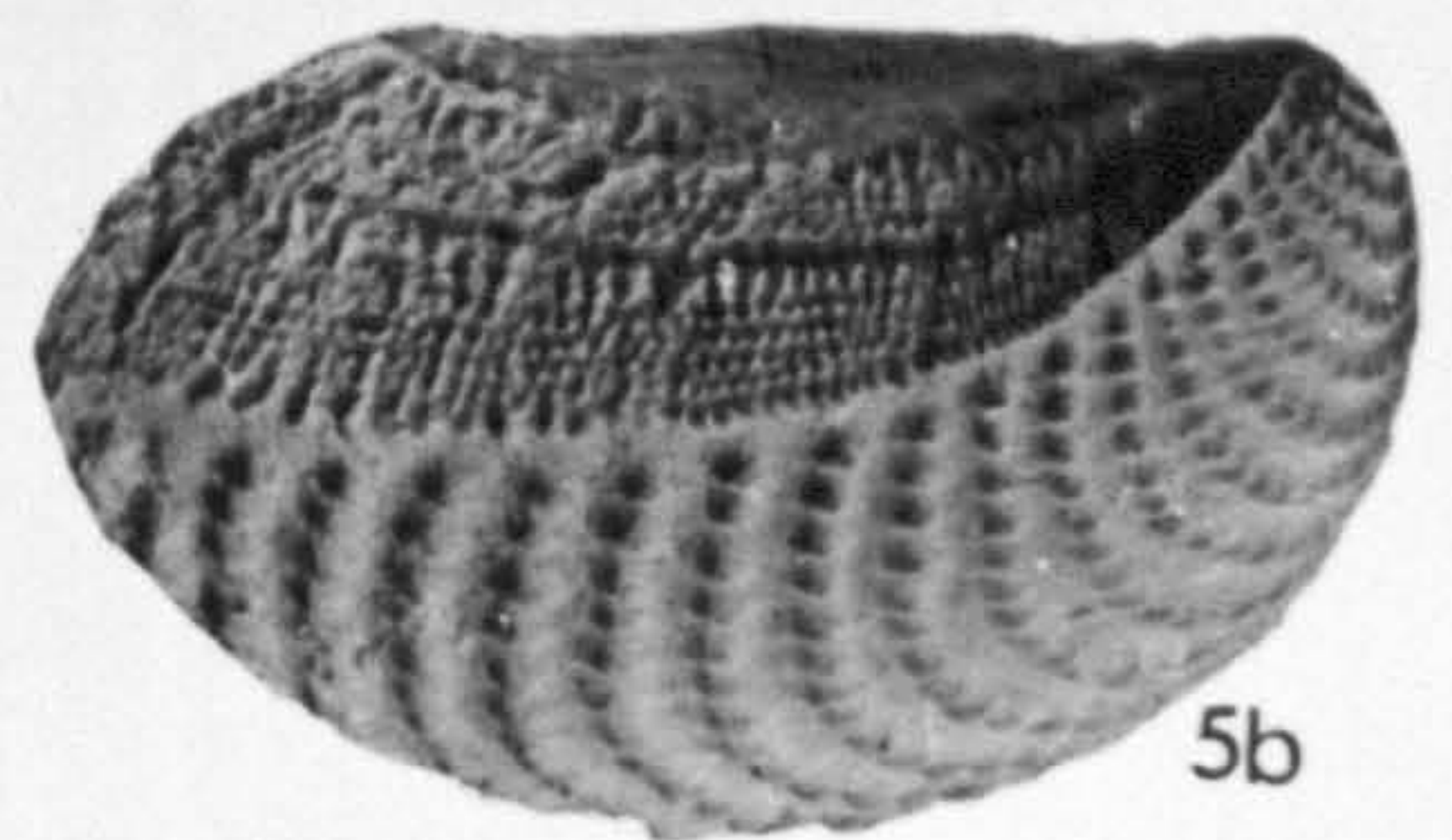
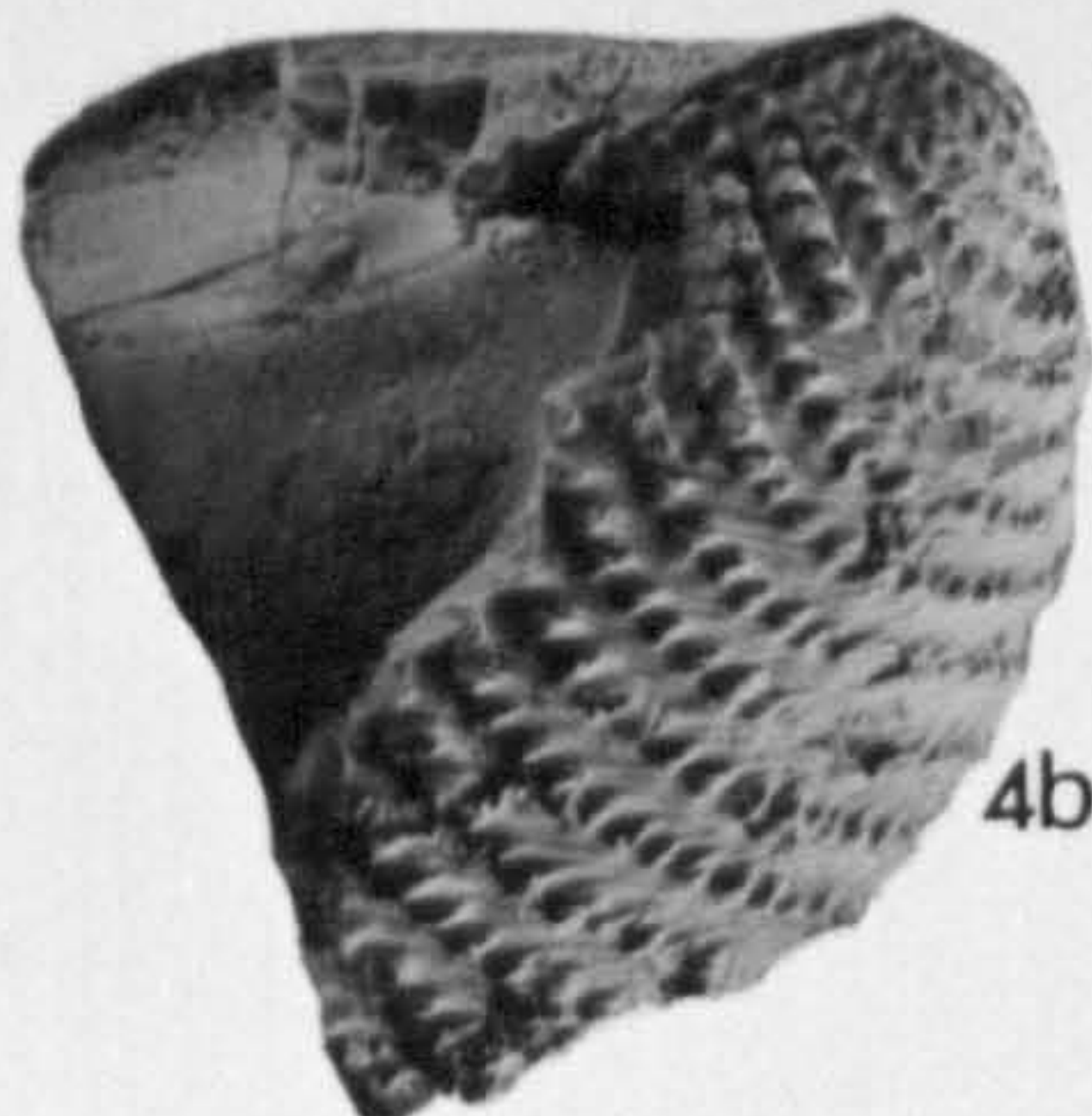
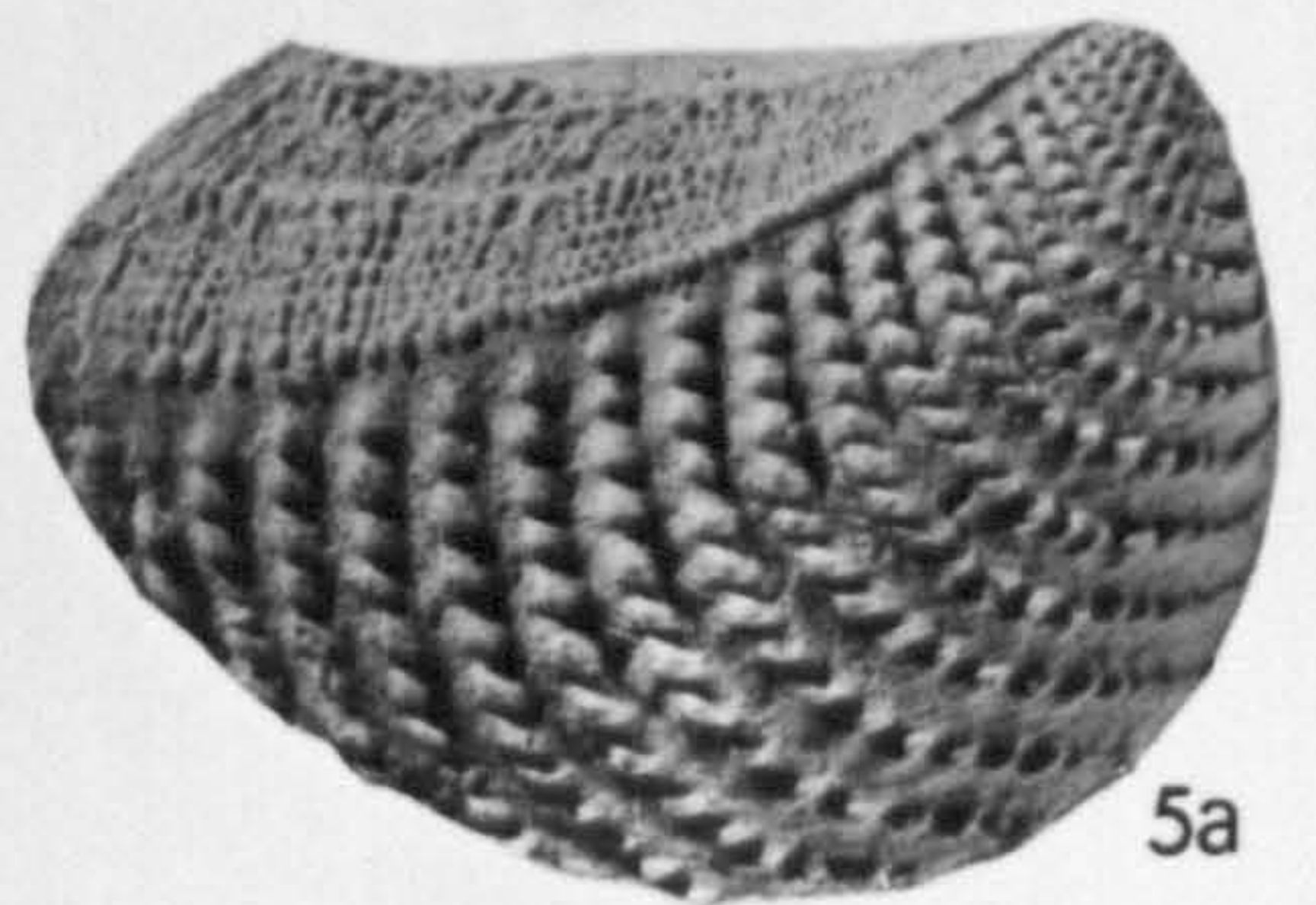
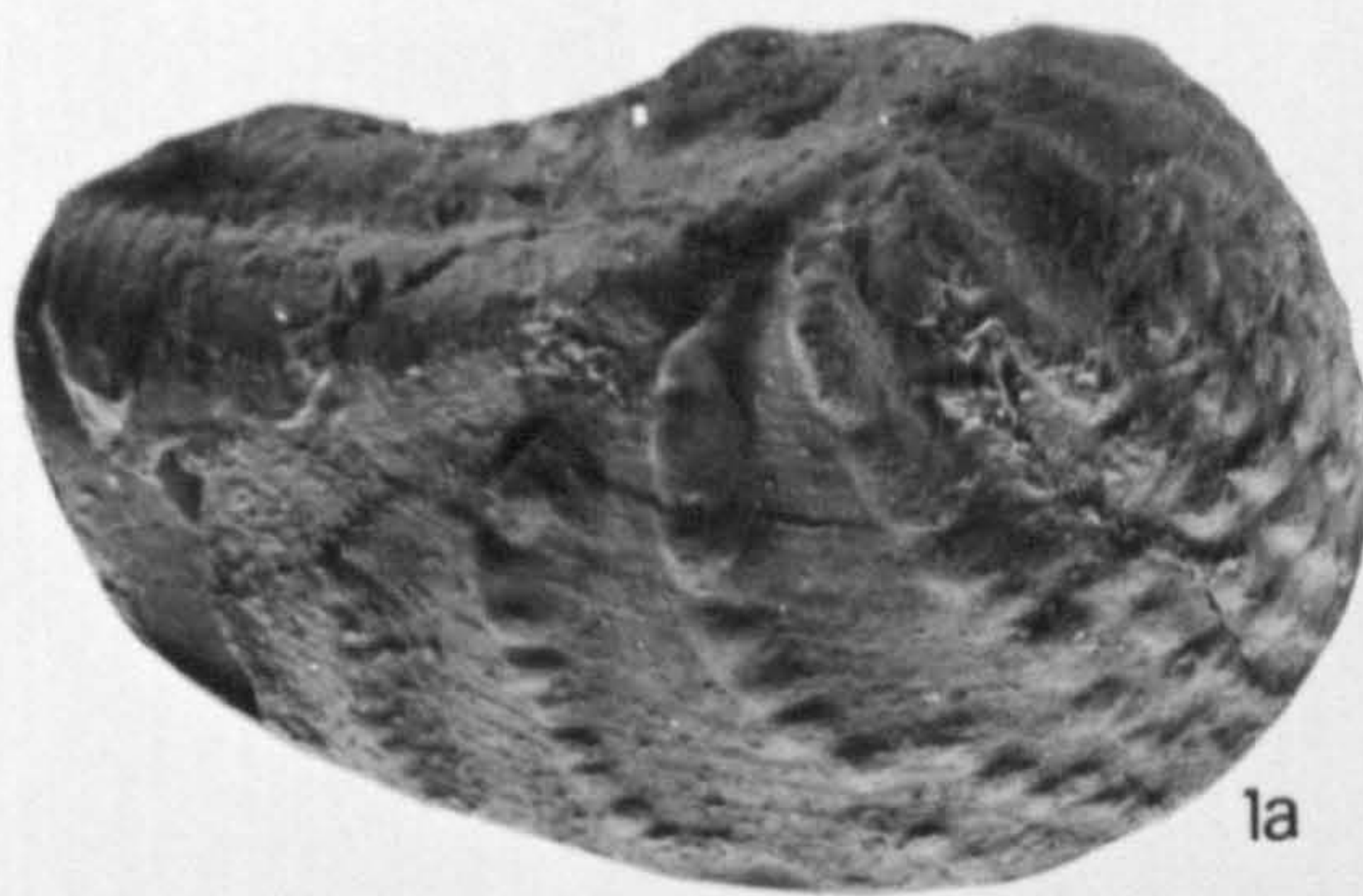
EXPLANATION OF PLATE 13

Figs. 1a, b, 3. Iotrigonia atlantica sp. nov. 1a, b, holotype, SRAK JG.1666, right valve, basal conglomerate of Muslingeelv Member, Hesteeelv Formation, H. kochi Zone, Ryazanian, 3km south of Crinoidbjerg, South Jameson Land, East Greenland (Locality 308 of Spath, 1947). 3, paratype, ICS CE 1554, silicone rubber cast of right valve, Mintlyn Beds, H. kochi Zone, Ryazanian, West Dereham Flood Relief Channel, Norfolk.

Fig. 2. Iotrigonia cf. atlantica sp. nov. ICS CE 3228, silicone rubber cast of right valve, erratic block of Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, Leziate, Norfolk.

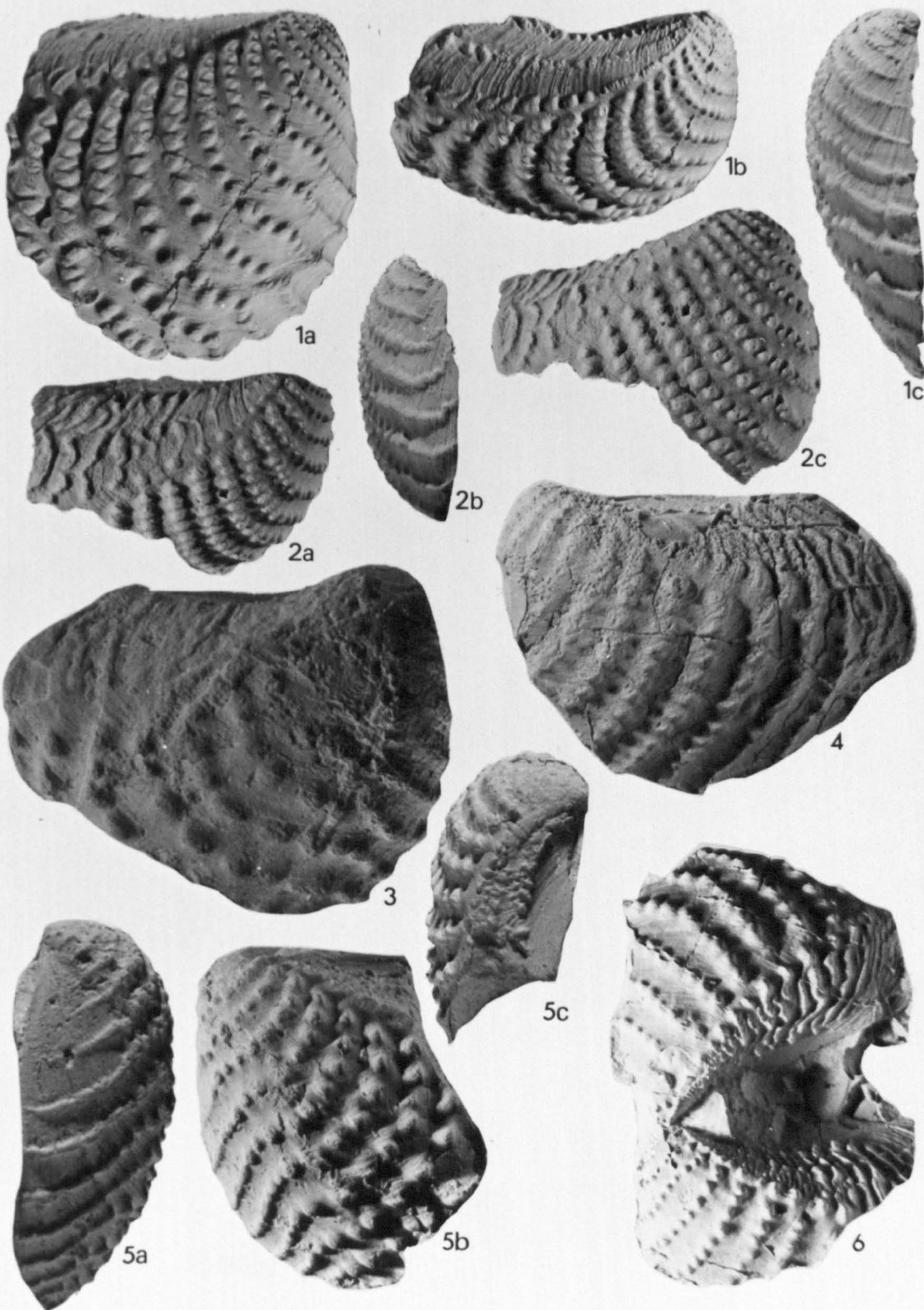
Figs. 4a, b, 5a-d, 6, 7a-c. Myophorella (Myophorella) tealbyensis (Lycett). 4a, b, SMC B.11241, holotype, incomplete right valve, Spilsby Sandstone, unhorizoned, Tealby, Lincs; 5a-d, SRAK IG.2490, silicone rubber cast of right valve; 7a-c, IG.2493, silicone rubber cast of right valve, Bed 1 calcareous concretions, Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, High Barn, West Keal, Lincs. 6, ICS CE 3263, silicone rubber cast of left valve, erratic block of Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, Leziate, Norfolk.

PLATE 13



EXPLANATION OF PLATE 14

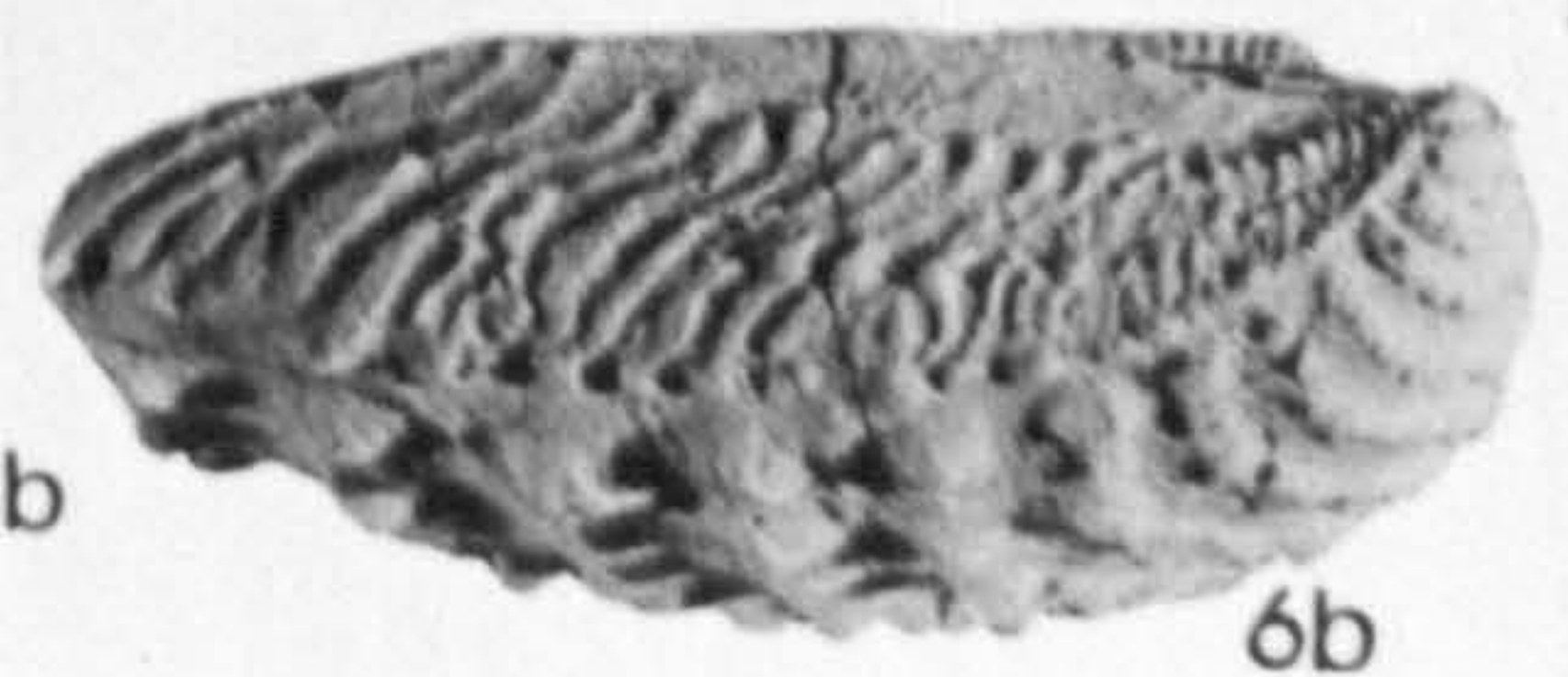
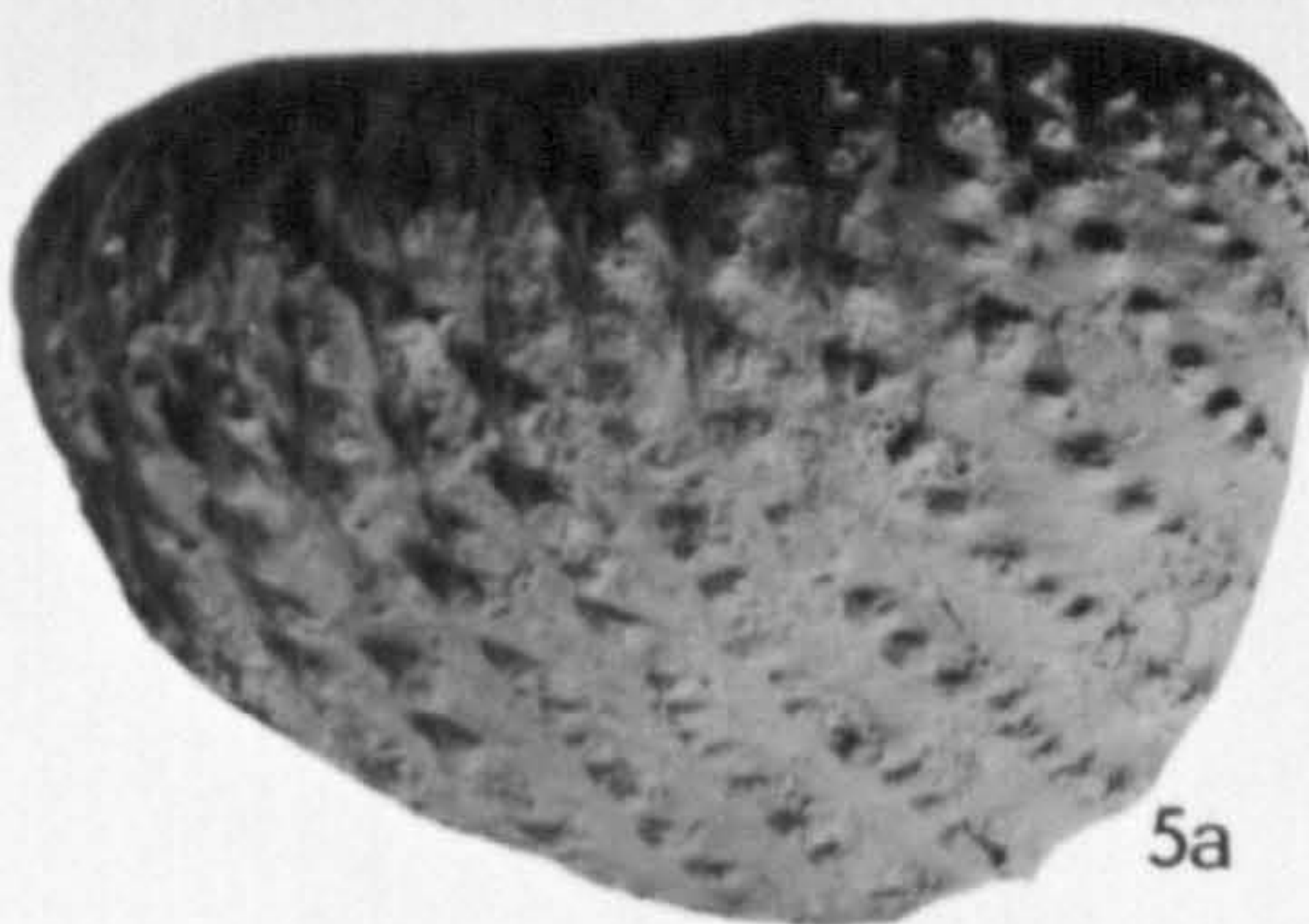
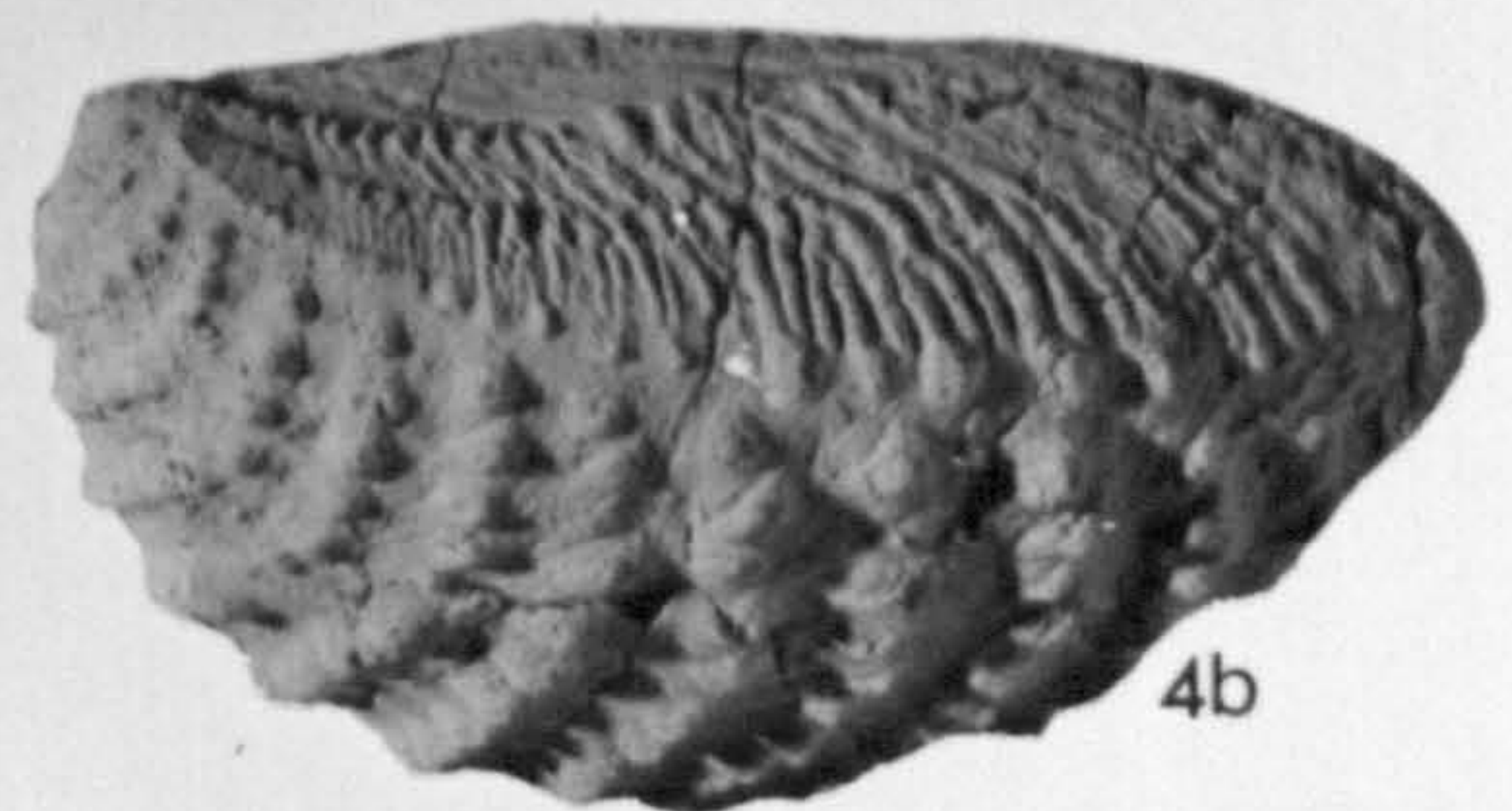
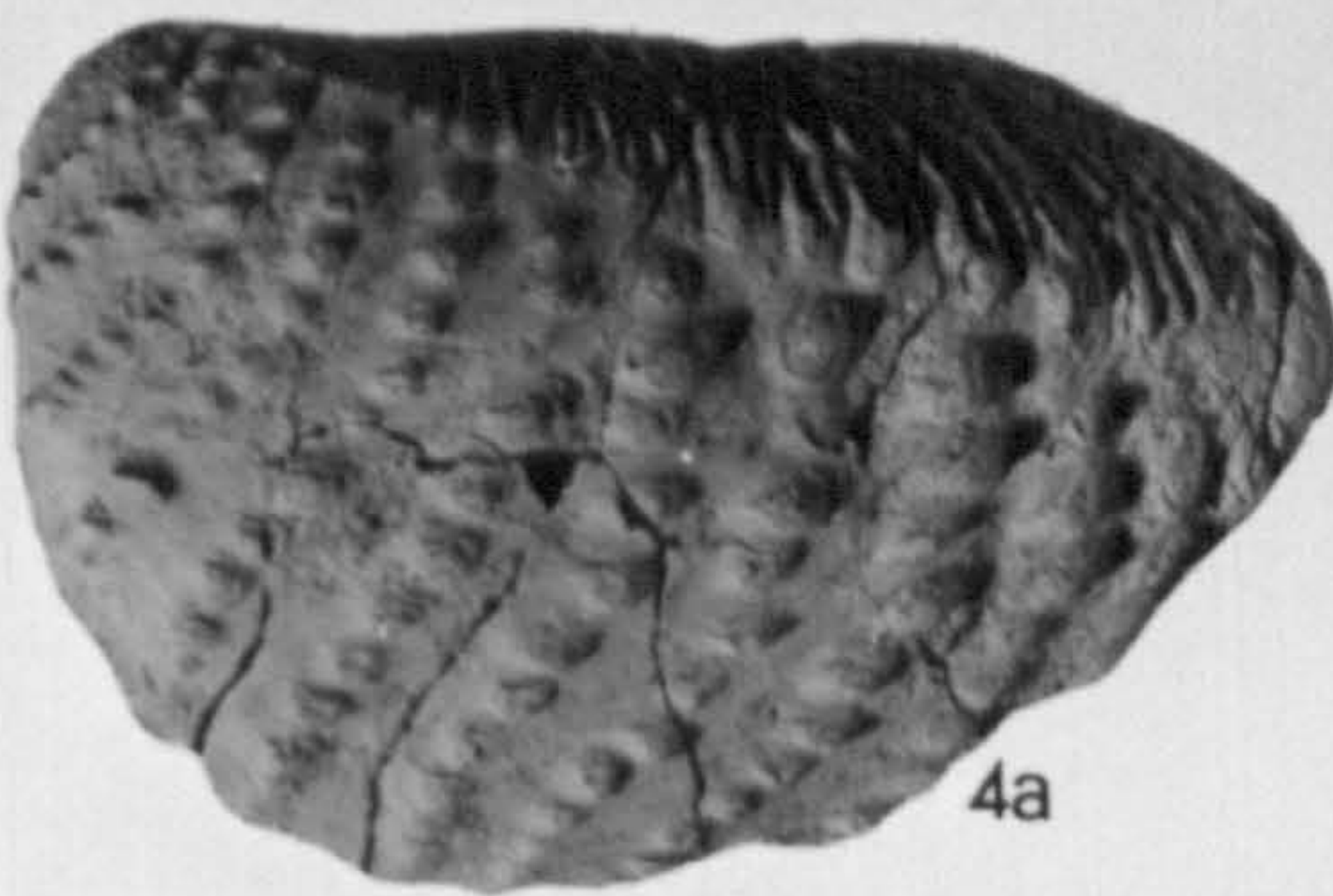
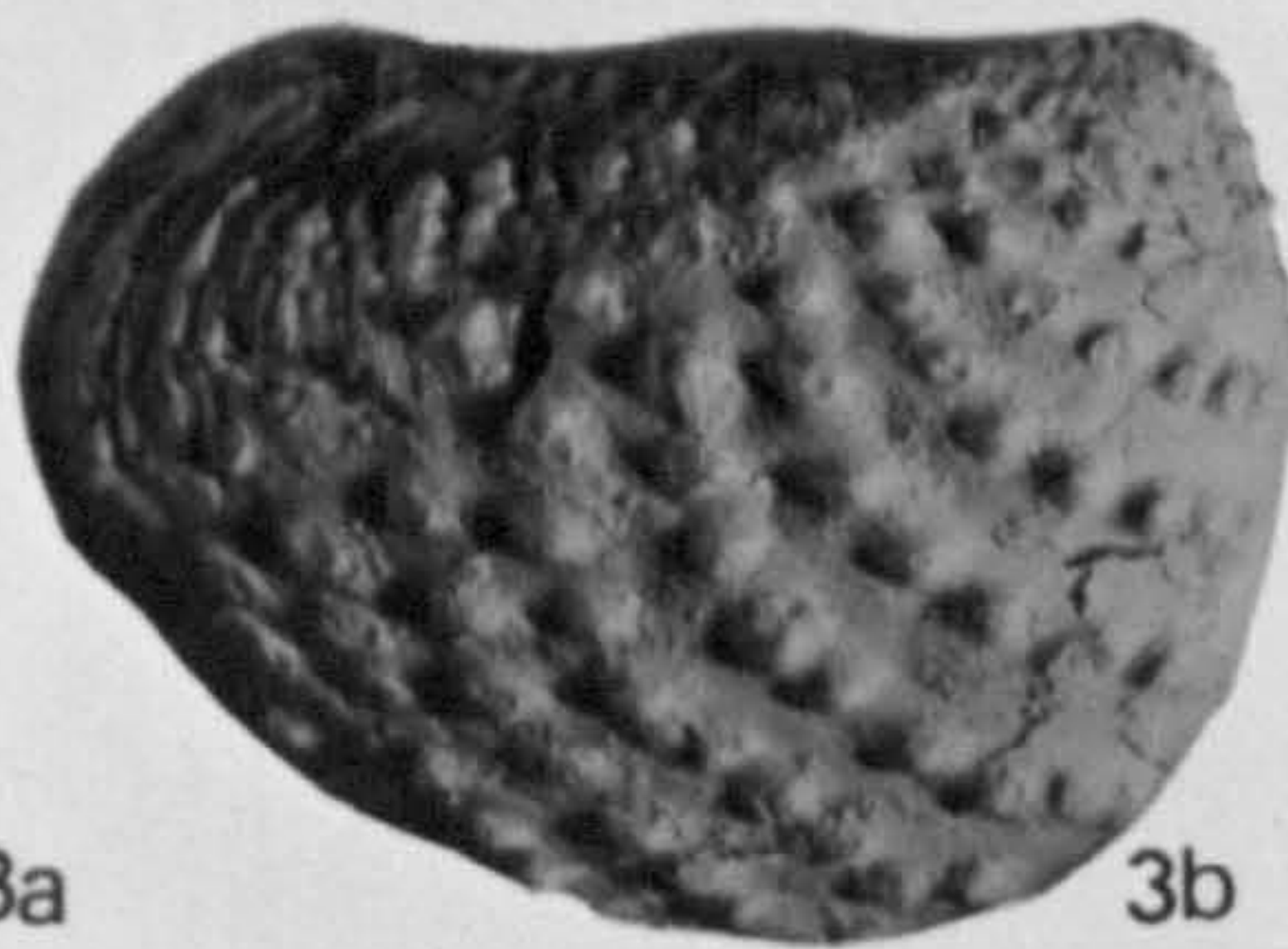
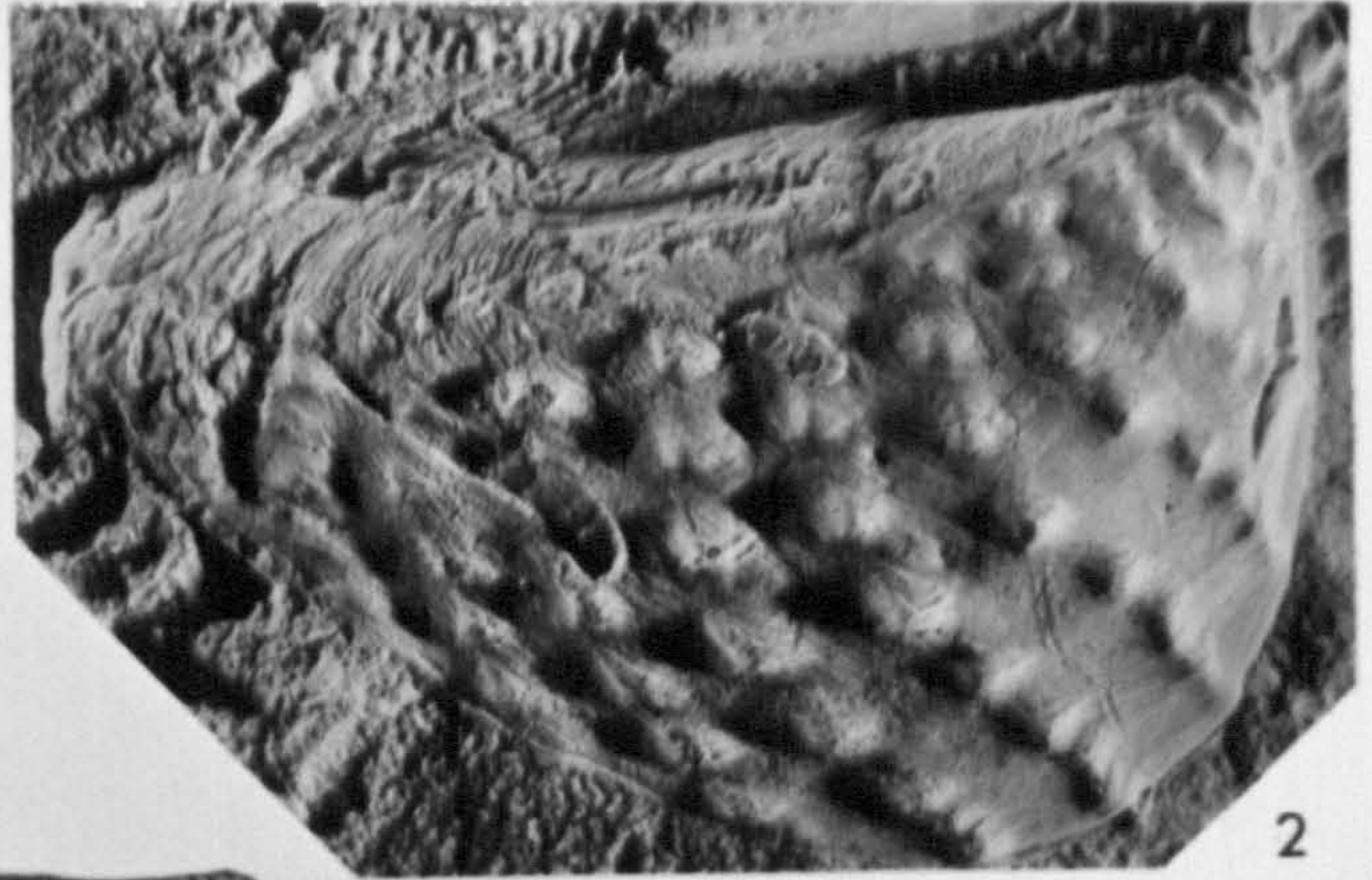
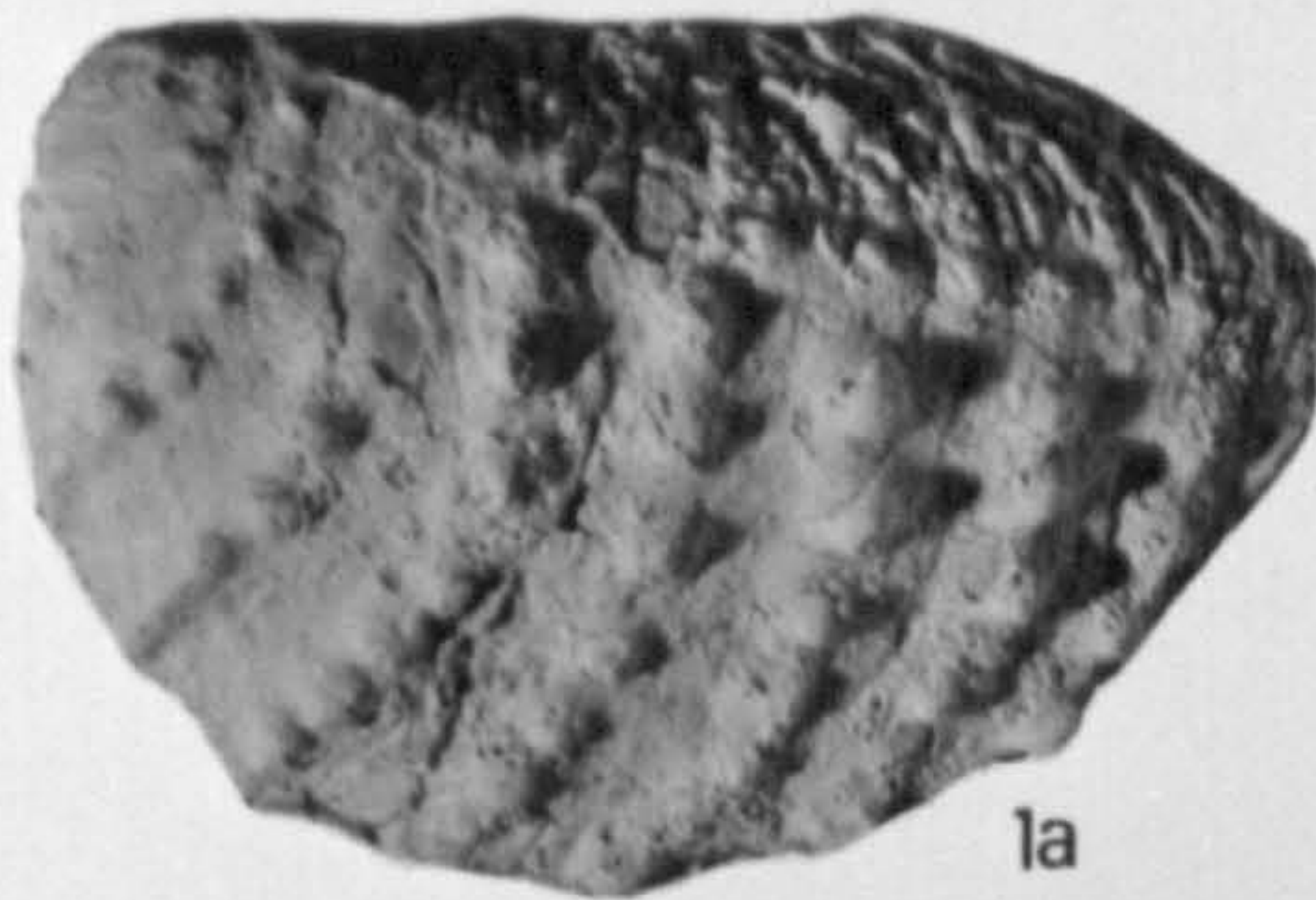
Figs. 1a-c, 2a-c, 3, 4, 5a-c, 6. Myophorella (Myophorella) keepingi (Lycett). 1a-c, SMC B.11235, syntype, right valve (originally figured by Lycett, 1877, pl. 35, fig. 1); 2a-c, B.11236, lectotype, (originally figured by Lycett, 1877, pl. 35, fig. 2), Spilsby Sandstone, unhorizoned, Tealby, Lincs. 3, IGS CE 1563, silicone rubber cast of right valve; 5a-c, CE 1558, silicone rubber cast of left valve, Mintlyn Beds, H. kochi Zone, Ryazanian, West Dereham Flood Relief Channel, Norfolk. 4, CE4701, silicone rubber cast of left valve; 6, CE 4529, silicone rubber cast of gaping valves, Bed 10, Mintlyn Beds, S. stenomphalus Zone, Ryazanian, Mintlyn Wood, Norfolk.



EXPLANATION OF PLATE 15

Figs. 1a, b, 2, 3a-c, 4a-c, 5a, b, 6a-c. Paratypes of Myophorella
(Myophorella) claxbyensis sp. nov. 1a, b, CRAK KY.1073, left valve;
4a-c, KY.701, left valve; 5a, b, KY.787, right valve; 6a-c, KY.1077,
right valve, 1.5m above base of Claxby Ironstone associated with
Pseudogarrineria, Valanginian, Benniworth Haven Railway Cutting, Lincs.
2, NLF3, uncatalogued, composite internal mould of right valve,
Mittel Valangian, Lindhorst, West Germany. 3a-c, KY.106, right valve,
loose specimen from lower part of the Claxby Ironstone, Nettleton,
Lincs.

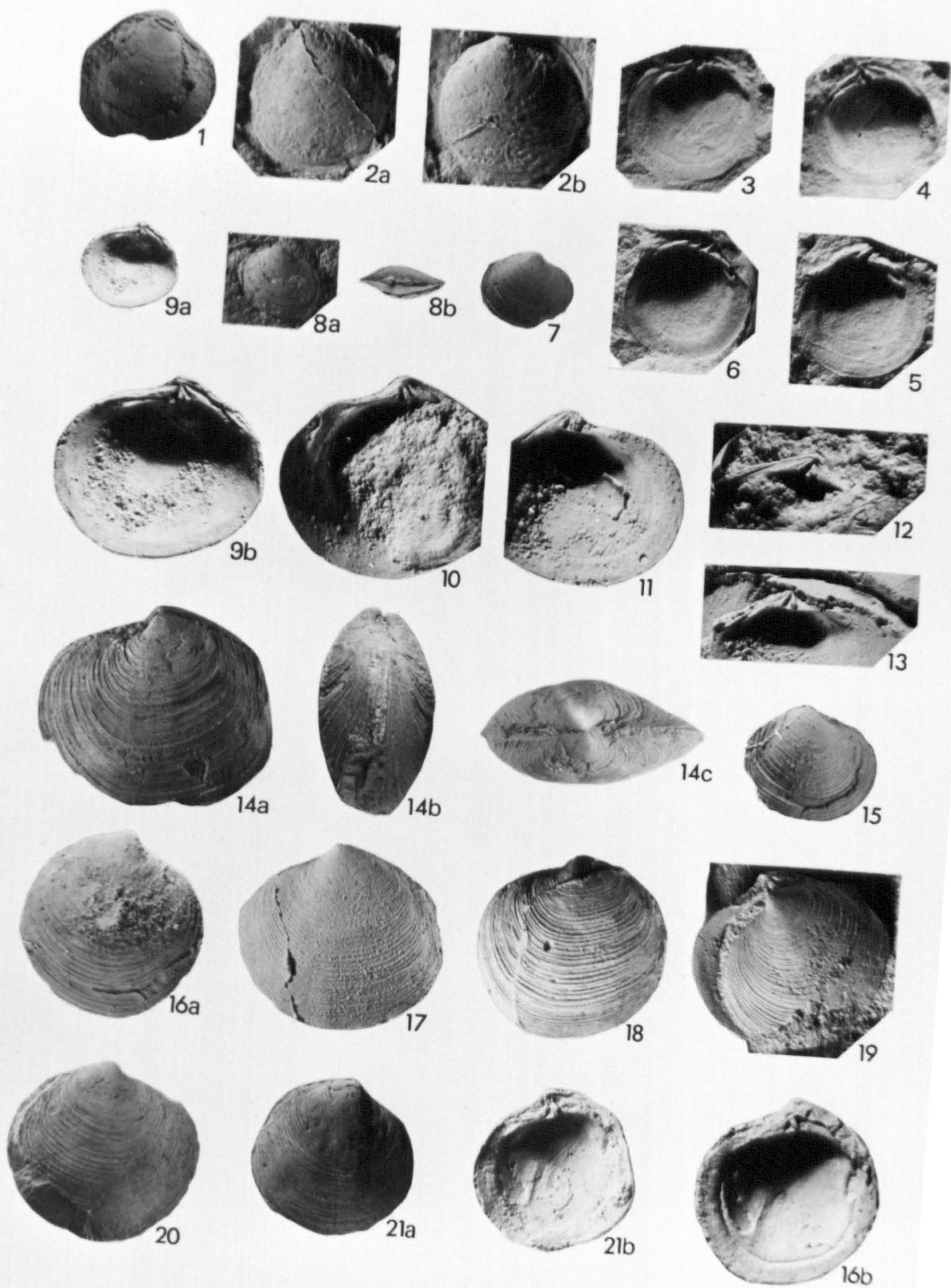
PLATE 15



EXPLANATION OF PLATE 16

Figs. 1, 2a, b, 3-6. Coinkia? crassa (J. de C. Sowerby). 1, SRAK IG.629, right valve exterior showing radial ornament; 2a, b, IG.629, silicone rubber casts of right and left valve exteriors respectively; 3, IG.629, silicone rubber cast of right valve interior; 6, IG.1742, silicone rubber cast of left valve interior; 3, 4, IGS CE 3453, neotype, silicone rubber casts of interior of right and left valves respectively, erratic blocks of Lower Spilsby Sandstone, P. oppressus Zone, Middle Volgian, Leziate, Norfolk.

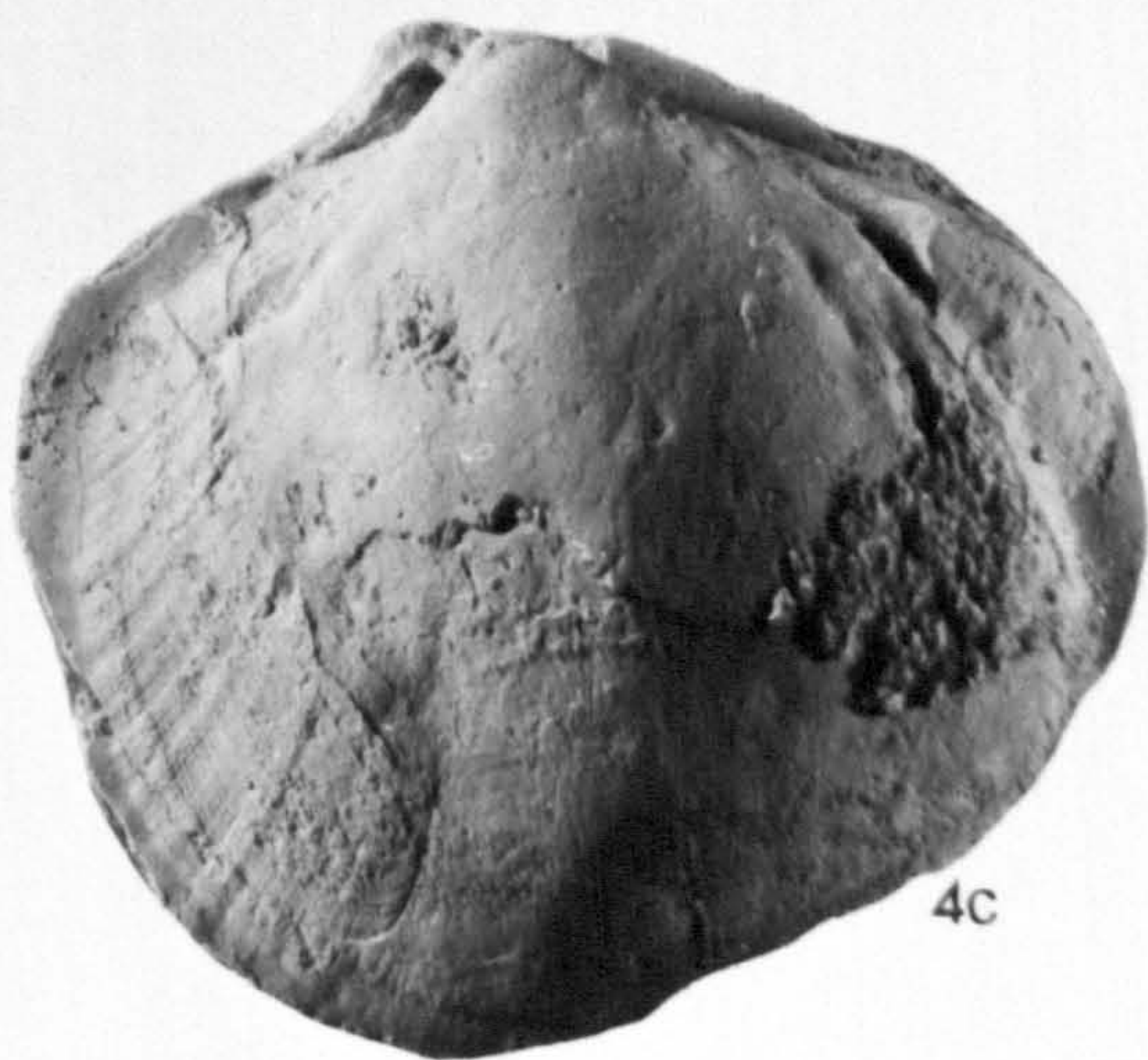
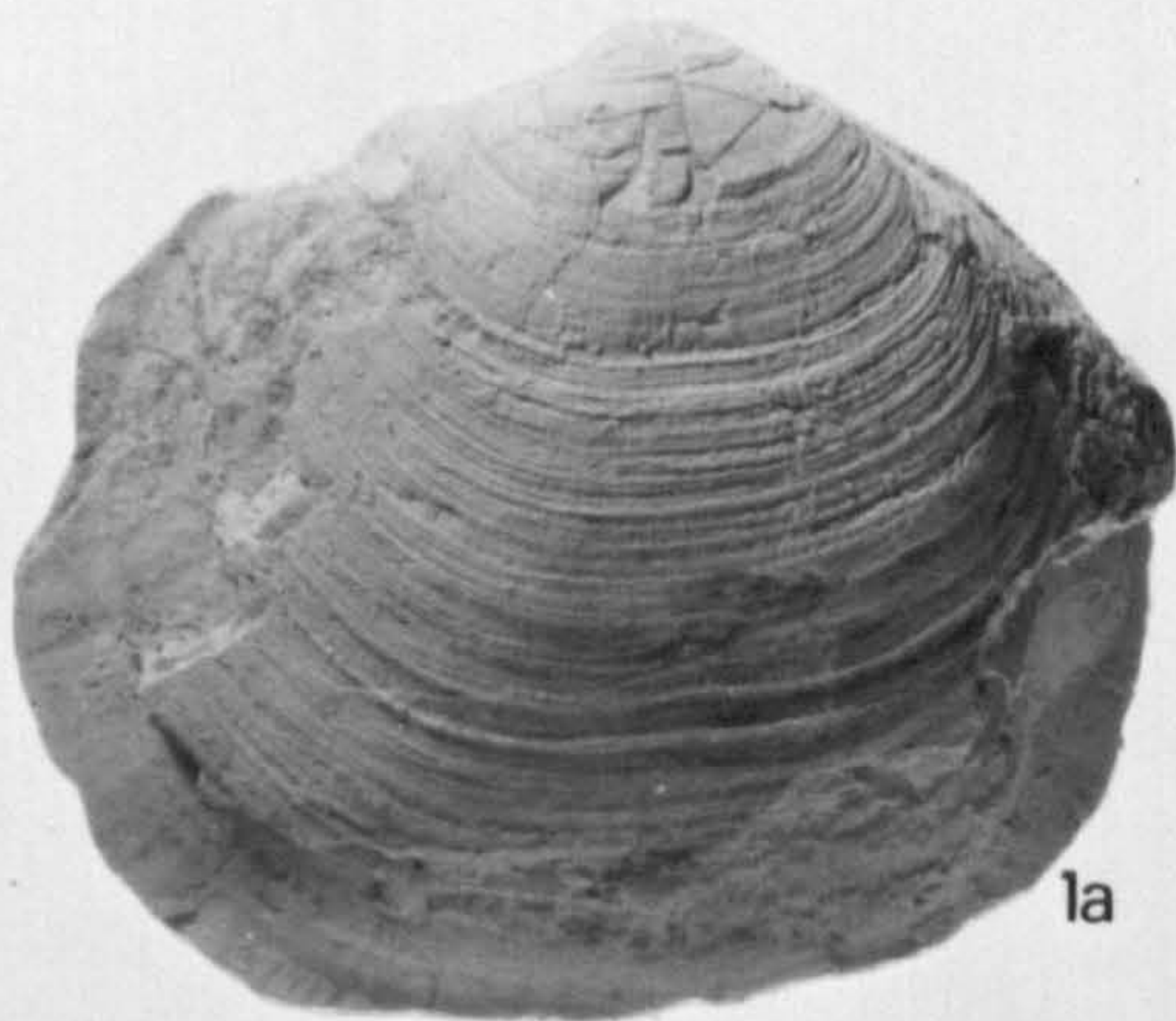
Figs. 7, 8a, b, 9a, b, 10-13, 14a-c, 15, 16a, b, 17-20, 21a, b. Discolorites fischerianus (d'Orbigny). 7, SRAK IG.2469, silicone rubber cast of right valve; 8a, b, IG.2480, silicone rubber cast, 8a, right lateral aspect, 8b, dorsal aspect; 9a, b, IG.2481, silicone rubber cast of right valve interior, 9b enlarged x3.2; 10, IG.2894, silicone rubber cast of right valve interior, enlarged x 3.2; 11, IG.2468, silicone rubber cast of left valve interior, enlarged x 3.2; 12, IG.2484, silicone rubber cast of left valve interior, enlarged x 3.2; 13, IG.2481, silicone rubber cast of left valve interior, enlarged x 3.2; 15, IG.2463, silicone rubber cast of right valve exterior; 16a, b, IG.3962, silicone rubber cast of right valve exterior and interior; 17, IG.2857, silicone rubber cast of left valve exterior; 18, IG.2344, silicone rubber cast of left valve exterior; 19, IG.2482, silicone rubber cast of sheared valves; 20, IG.2477, silicone rubber cast of right valve exterior, Bed 1 calcareous concretions, Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, High Barn, West Keal, Lincs. 21a, b, IG.3391, silicone rubber cast of right valve exterior and interior, Bed 2 concretions, Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, 600m west of Harrington Hall, Lincs. 14a-c, IGS R26/87 complete individual with valves occluded. Spilsby Sandstone, unhorizoned, Old Bolingbroke Church, Lincs.



EXPLANATION OF PLATE 17

Figs. 1a-c, 2, 3, 4a-c, 5. Discoloripes septentrionalis sp. nov.

1a-c, paratype, IHGPC 137417, complete individual, Glauconitic Series, Middle Volgian, Milne Land, East Greenland. 2, holotype, SRAK JG.1808, left valve detail of hinge. 3, paratype, JG.1795, hinge line of right valve; basal conglomerate, Muslingeelv Member, Hesteelv Formation J. Kopp Zone, Ryazanian, 3km south of Crinoidbjerg, South Jameson Land, East Greenland. 4a-c, paratype, IGS CE 3776, phosphatised steinkern; 5, paratype, CE 1929, phosphatised steinkern showing pits representing tubercles, Runcton Beds, S. lamplughii Zone, Upper Volgian, Roxham Farm, Norfolk.



EXPLANATION OF PLATE 18

Figs. 1-6. Mesomiltha? kostromensis (Gerasimov). 1, SRAK, IG. 527, silicone rubber cast of right valve; 2, IG.1751, composite internal mould of left valve; 3, IG.346, composite internal mould of left valve; 4, IG.521, composite internal mould of left valve, erratic blocks of Lower Spilsby Sandstone, E. oppressus Zone, Middle Volgian, Leziate, Norfolk. 5, IG.3420 silicone rubber cast of left valve exterior, Bed 1 concretion, Lower Spilsby Sandstone, S. prelicomphalus Zone, Upper Volgian, High Barn, West Weal, Lincs. 6, IG.2360, silicone rubber cast of left valve exterior, Bed 1, same horizon as fig. 5, 600m west of Harrington Hall, Lincs.

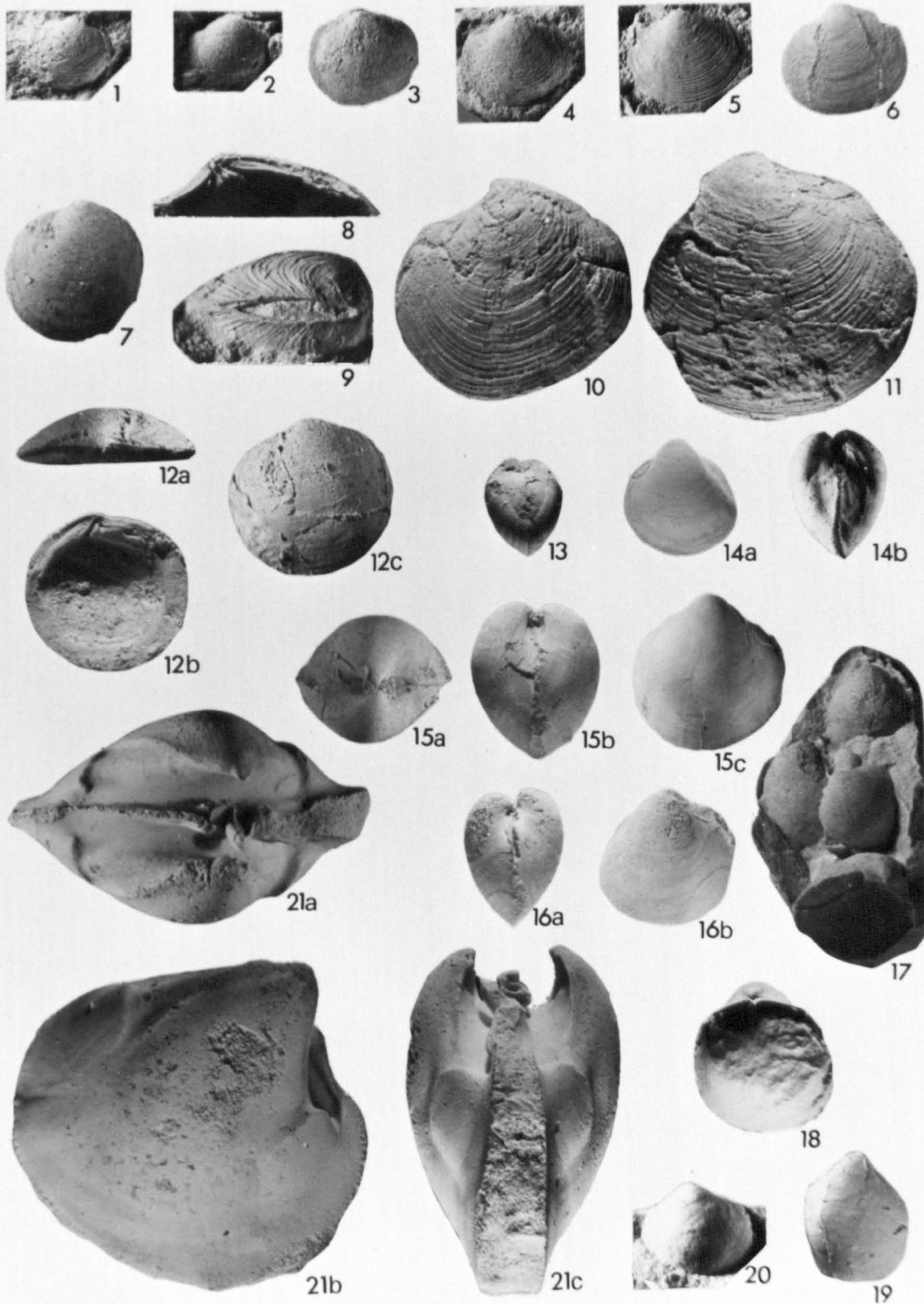
Figs. 7, 12a-c. Discoloripes sp. nov.? 7, SRAK IG.2490, silicone rubber cast of left valve exterior; 12a-c, IG. 2605, silicone rubber cast of left valve exterior and interior, Bed 1 concretions, Lower Spilsby Sandstone, S. prelicomphalus Zone, Upper Volgian, High Barn, West Keal, Lincs.

Figs 8-11. Discoloripes aff inequalis (d'Orbigny). 8, SRAK IG.2327, silicone rubber cast of right valve hinge; 9, IG.3372, silicone rubber cast of lunule; 10, IG.1844, silicone rubber cast of left valve exterior; 11, IG.1843, silicone rubber cast of right valve exterior, Bed 4, Lower Spilsby Sandstone, S. primitivus Zone, Upper Volgian, Nettleton, Lincs.

Figs. 13, 14a-b. Protocardia concinna Buch. 13, IGS CN 497, phosphatised shell, posterior aspect; 14a-c, CN 261, phosphatised steinkern, Basal Cretaceous nodule Bed, Mintlyn Beds, Constitution Hill, West Winch, Norfolk.

Figs. 15a-c, 16a, b, 17-20. Protocardia ? sp. 15a-c, SMC B.12116, steinkern; 16a, b, B.12120, steinkern; Spilsby Sandstone, unhorizoned, but probably Upper Spilsby Sandstone, Donnington, Lincs. 17, IGS CE 4851, silicone rubber cast of several valves; 18, CE 4870, silicone rubber cast of right valve interior; 20, CE 4852, silicone rubber cast of left valve exterior, Bed 11, Mintlyn Beds, S. stenomphalus Zone, Ryazanian, Mintlyn Wood, Norfolk. 19, CE 5480, silicone rubber cast of right valve exterior, Bed 11, Mintlyn Beds, S. stenomphalus Zone, Ryazanian, North Runcton, Norfolk.

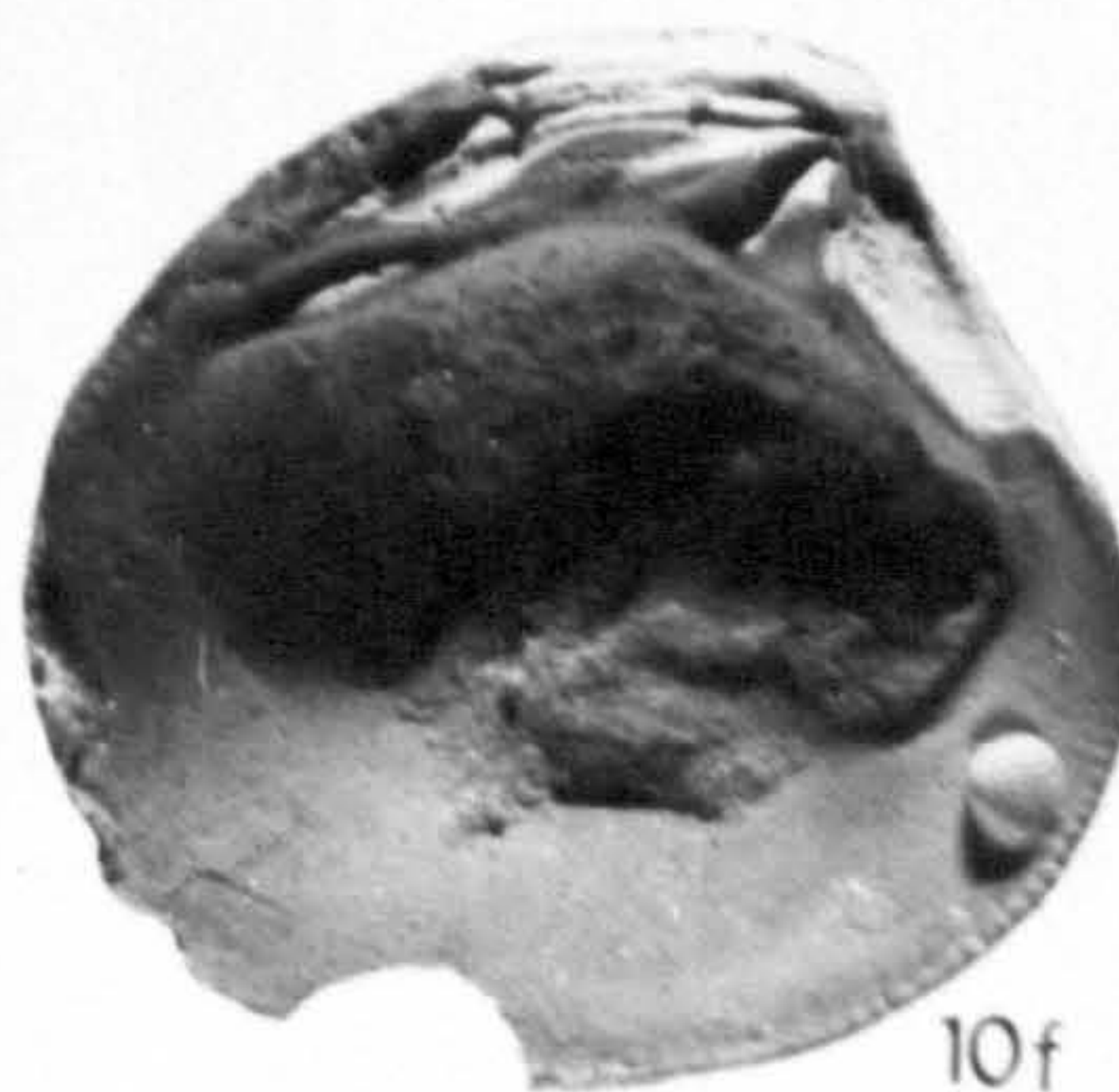
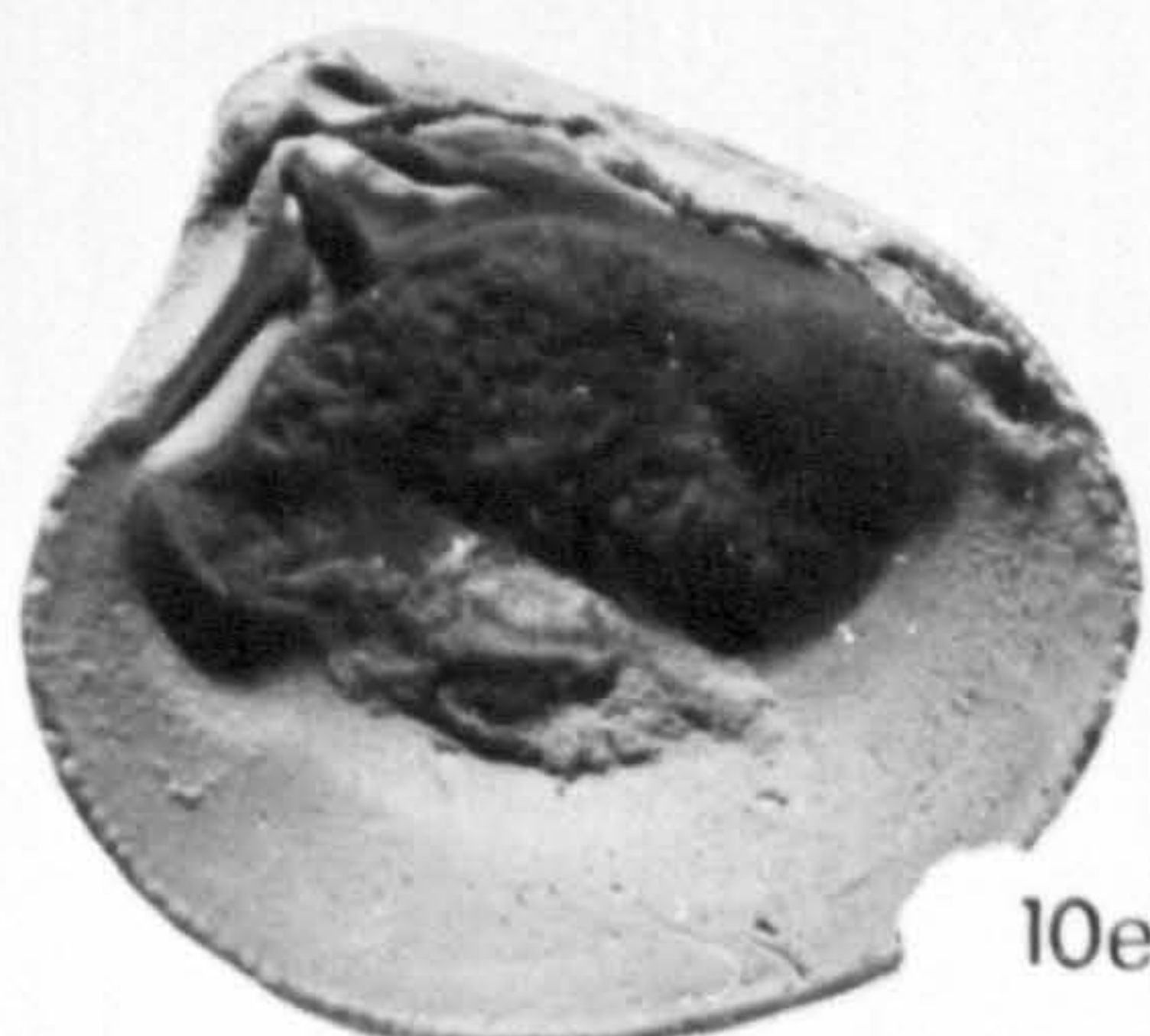
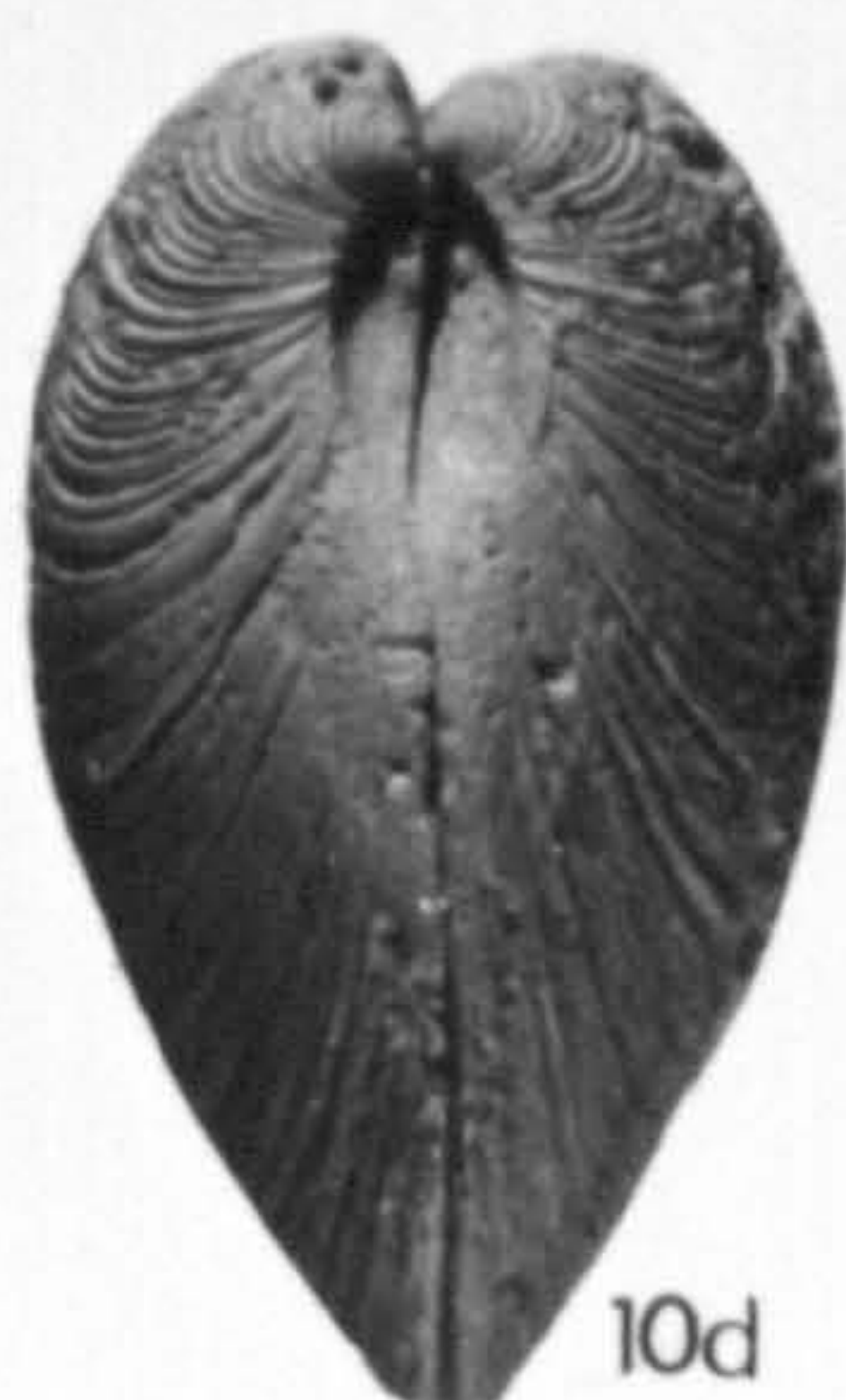
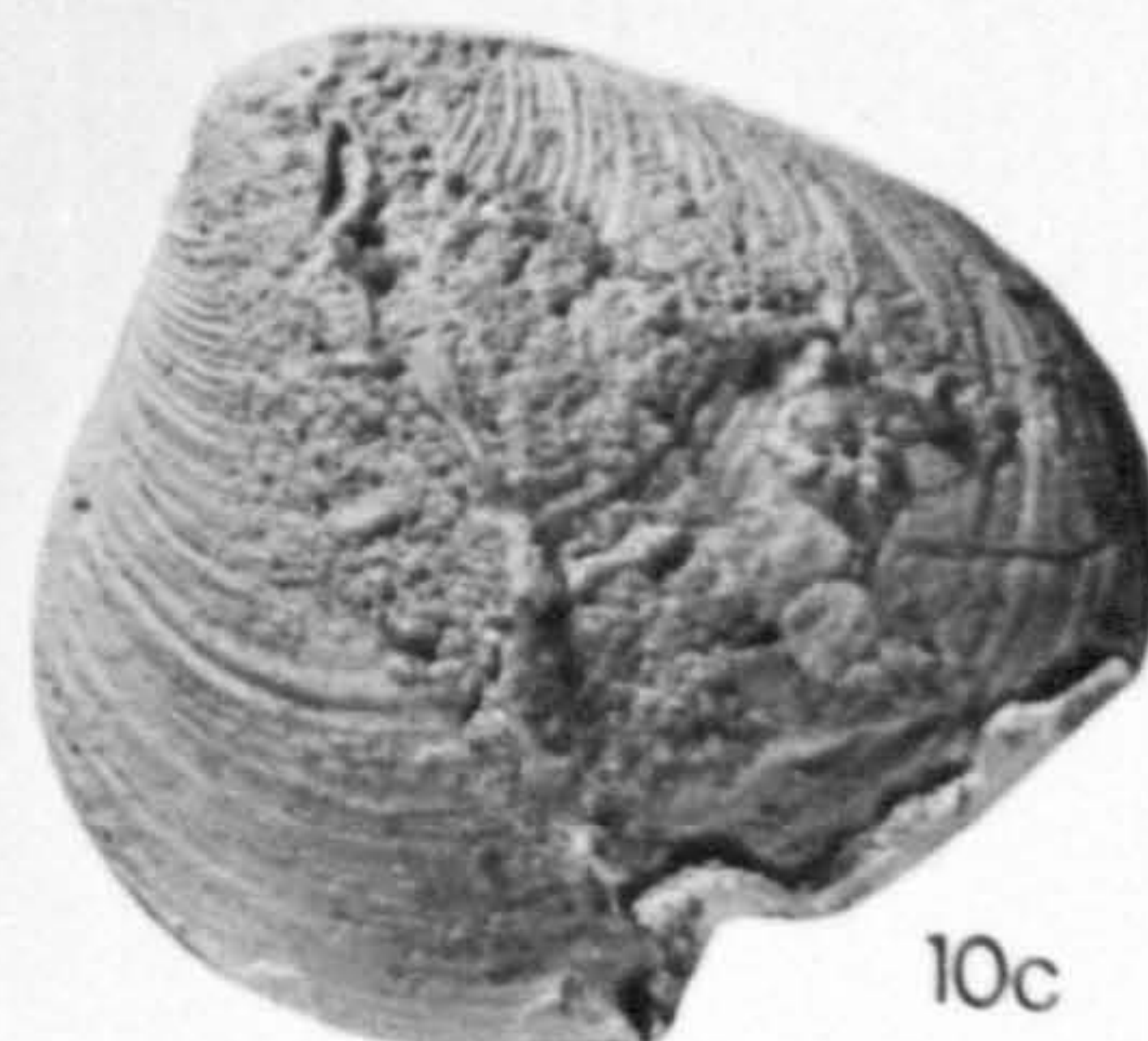
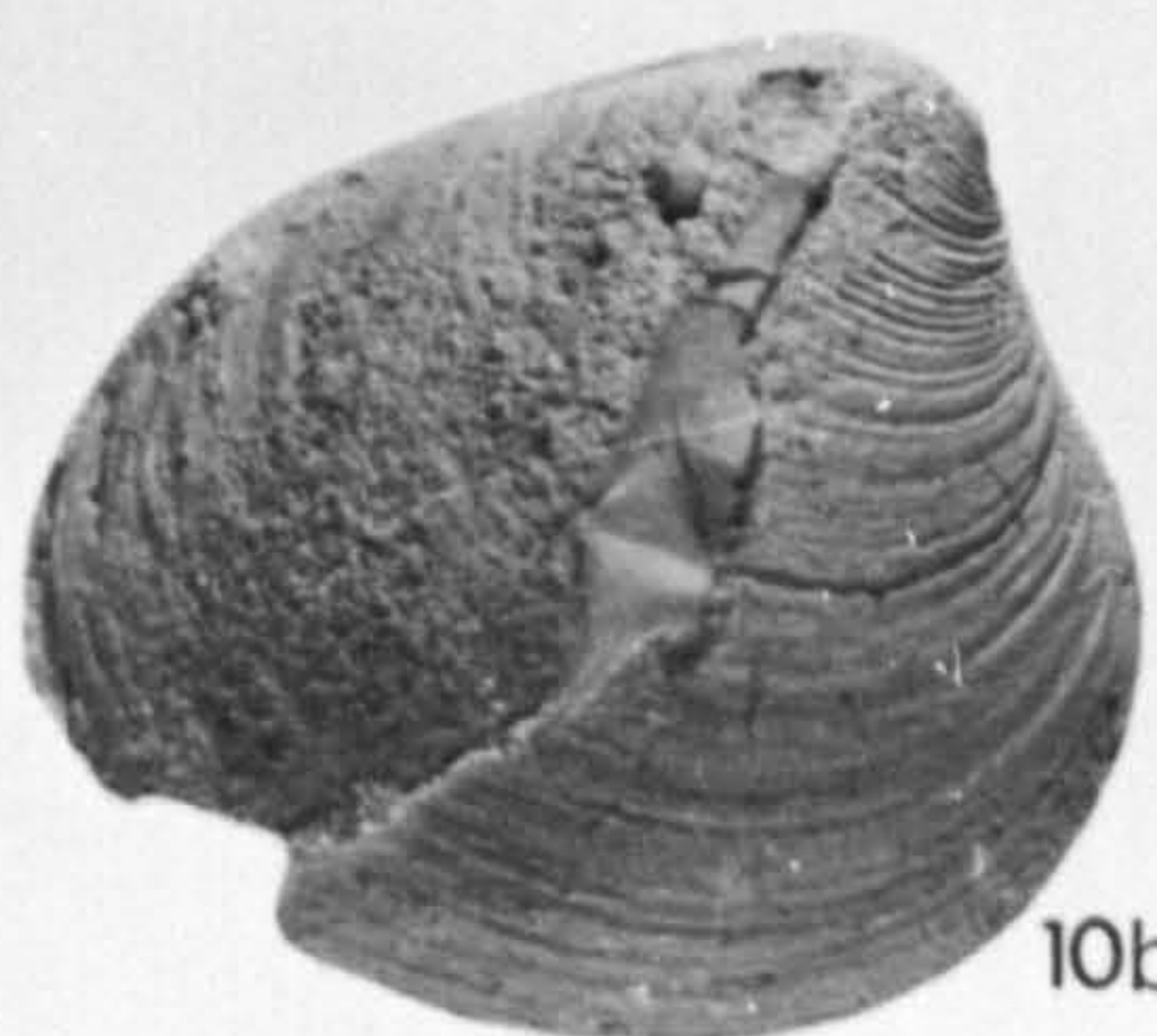
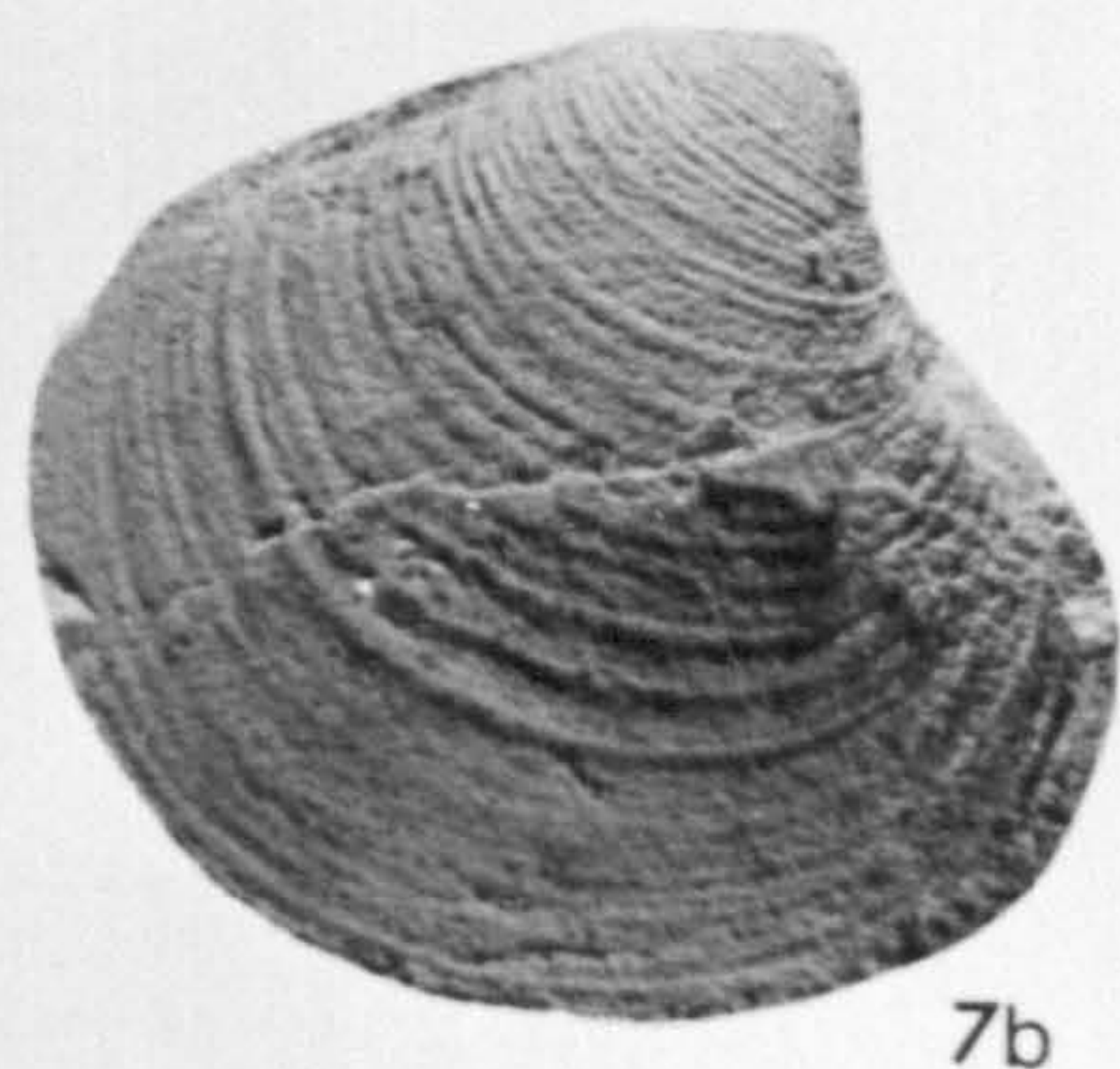
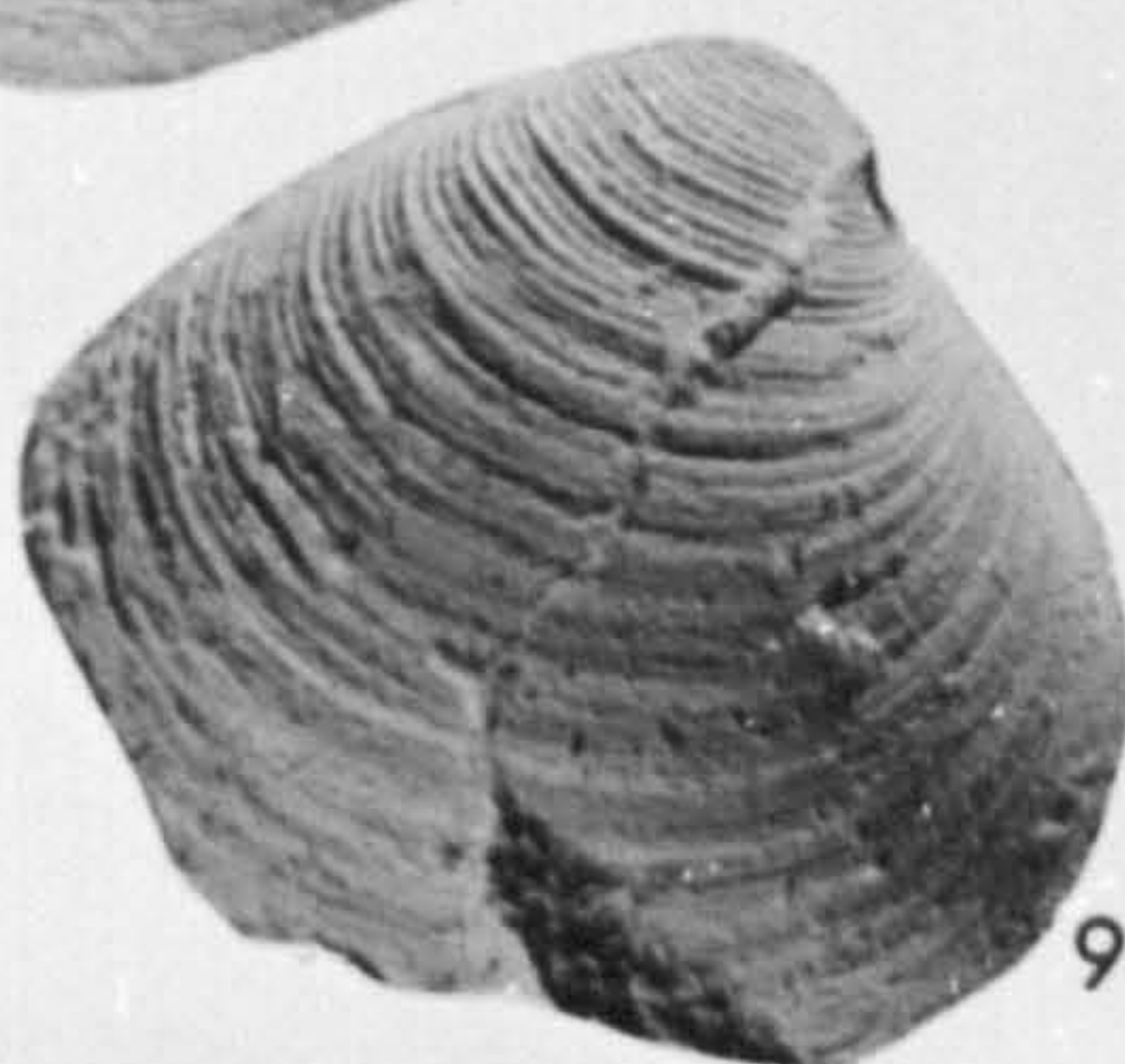
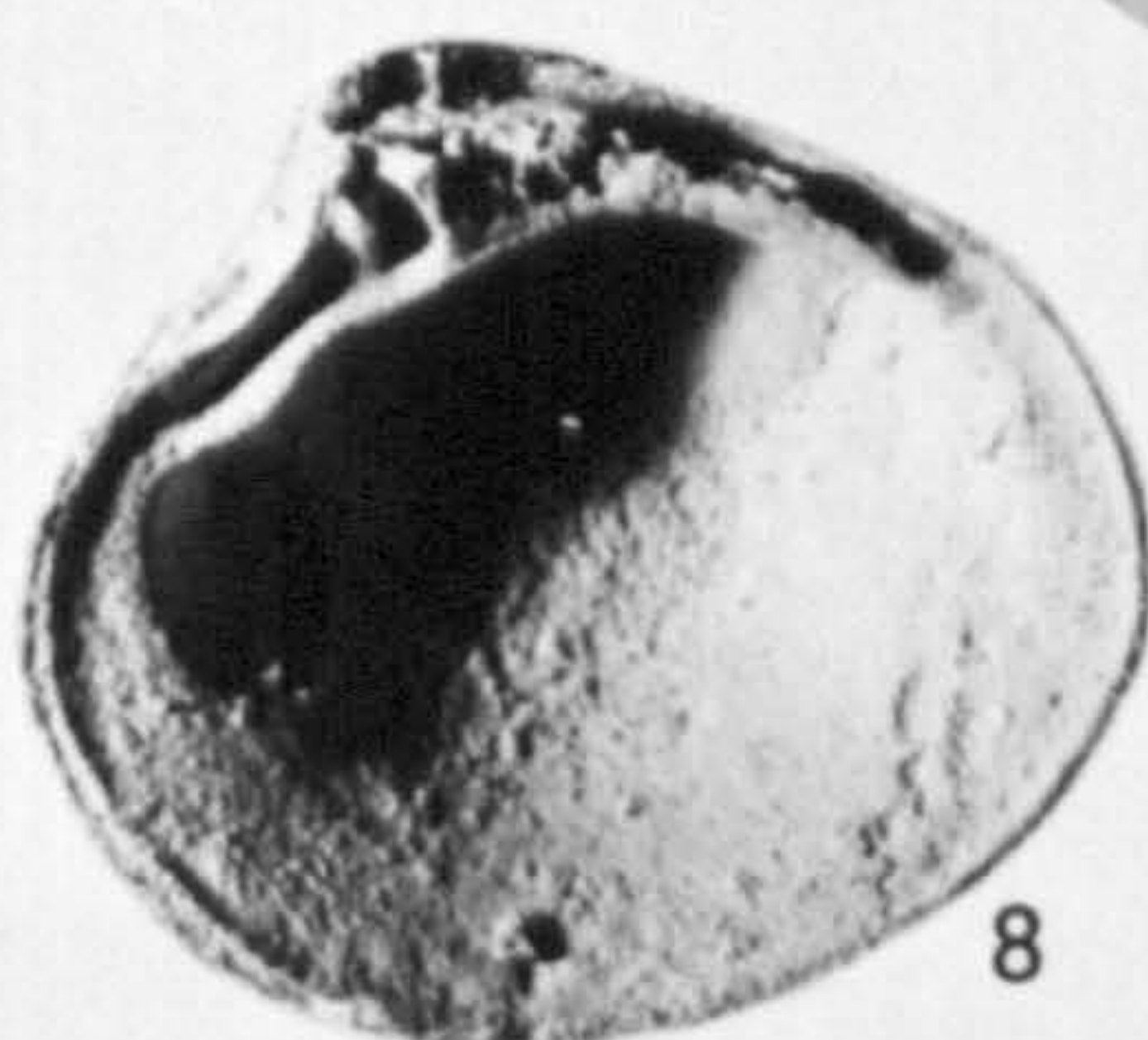
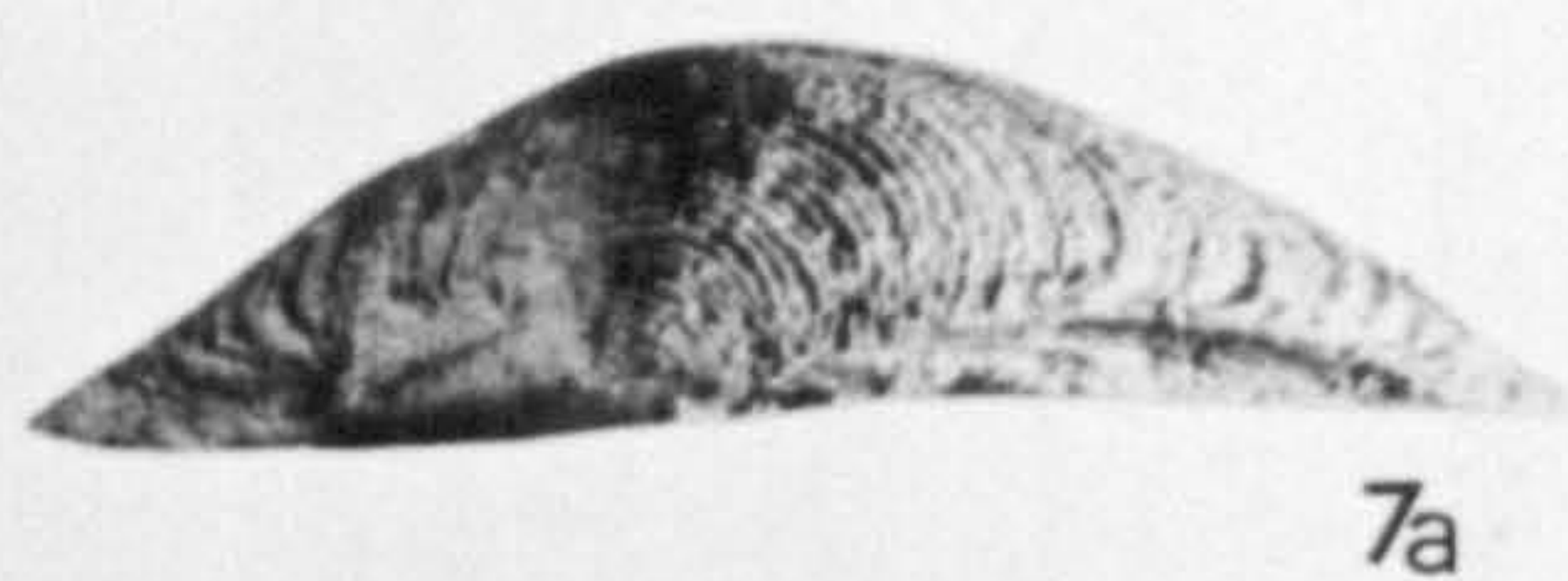
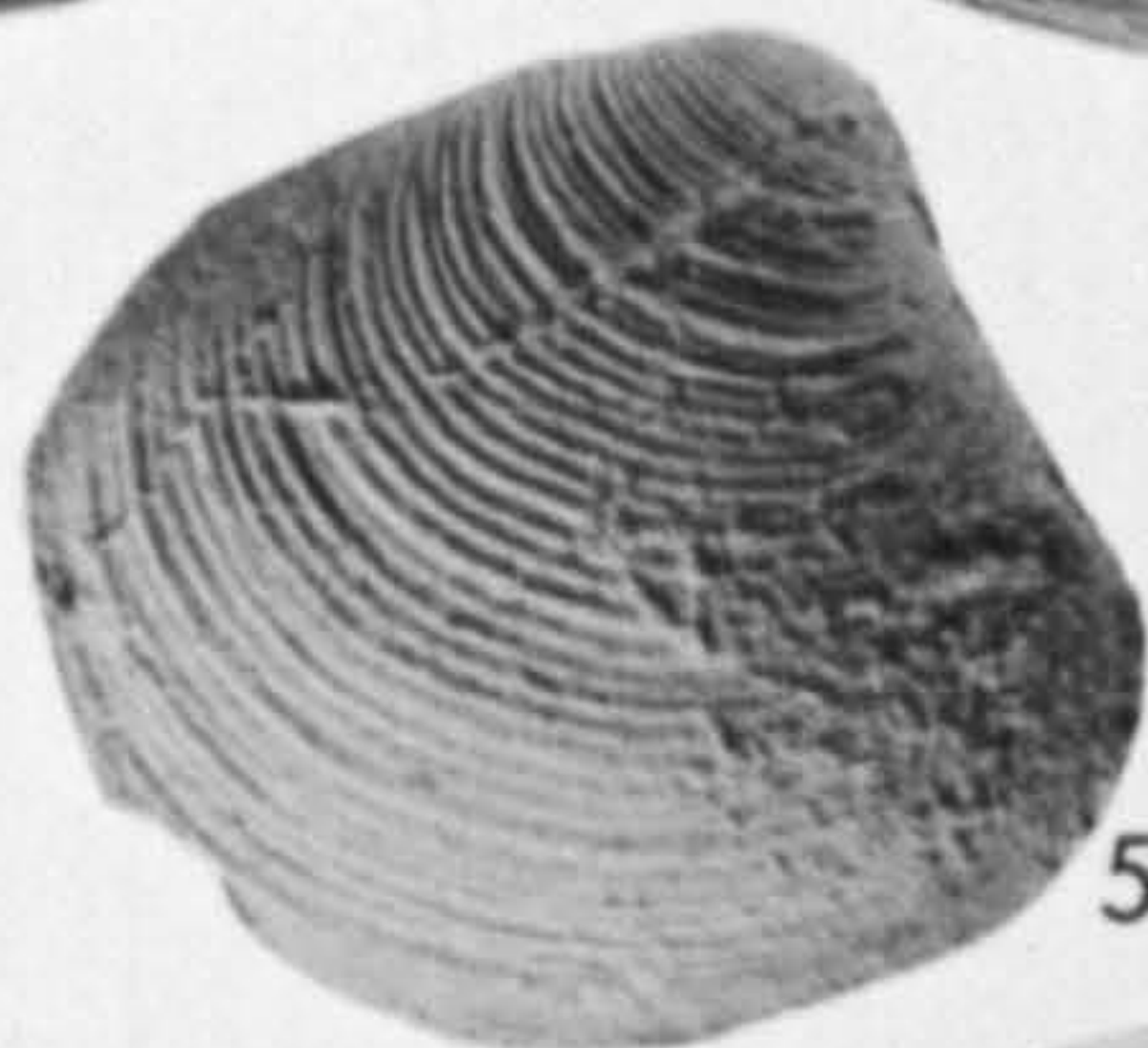
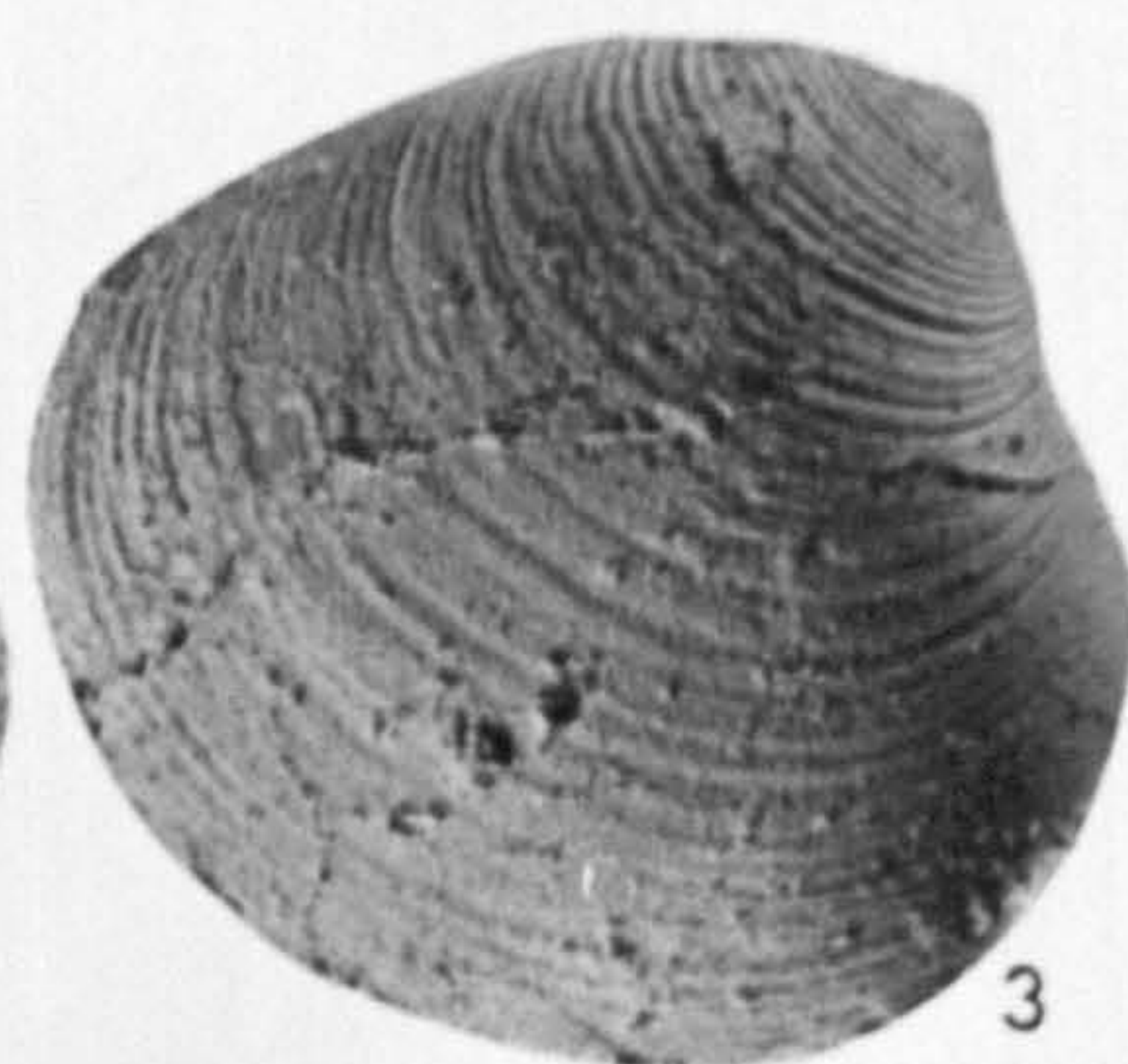
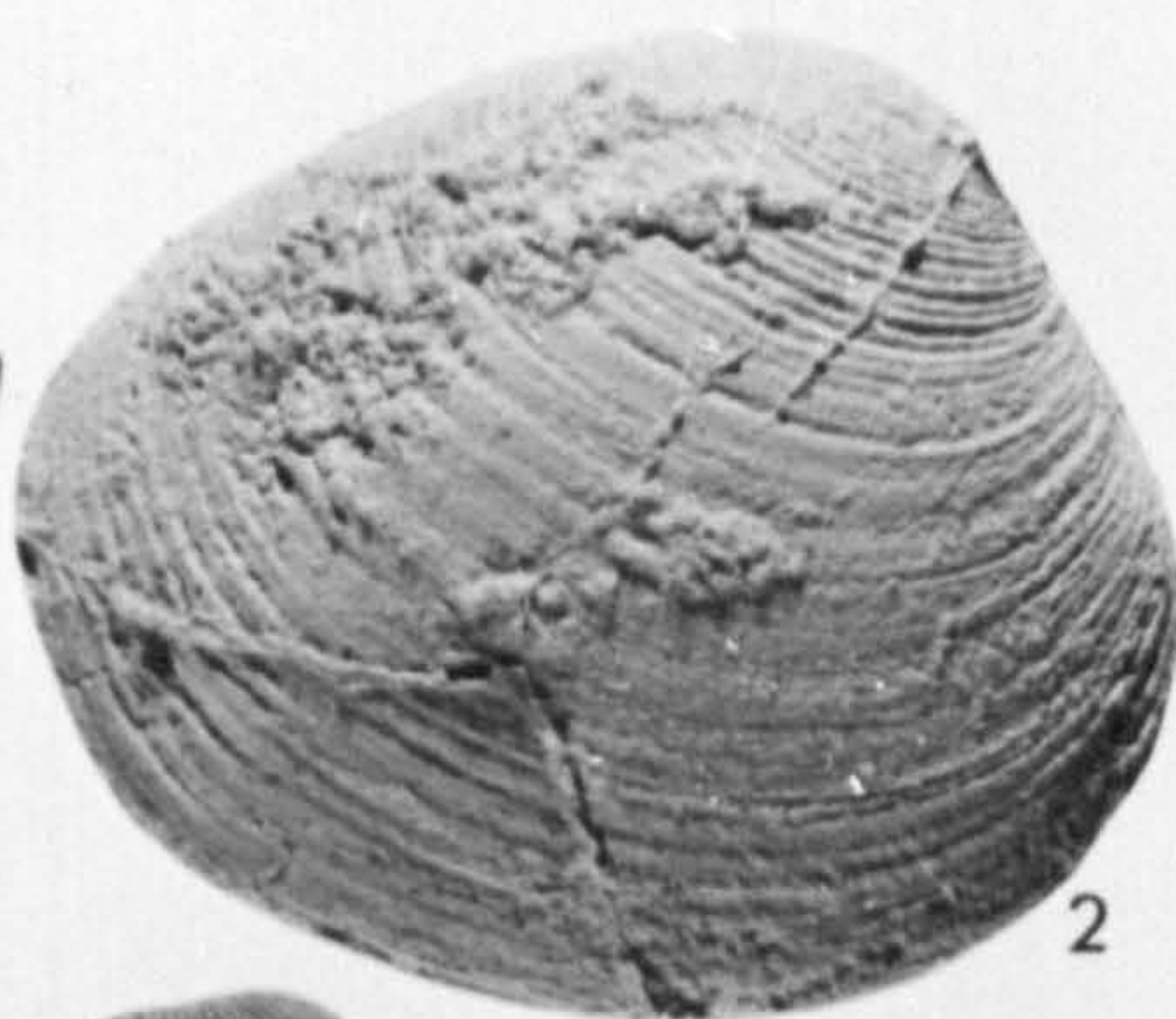
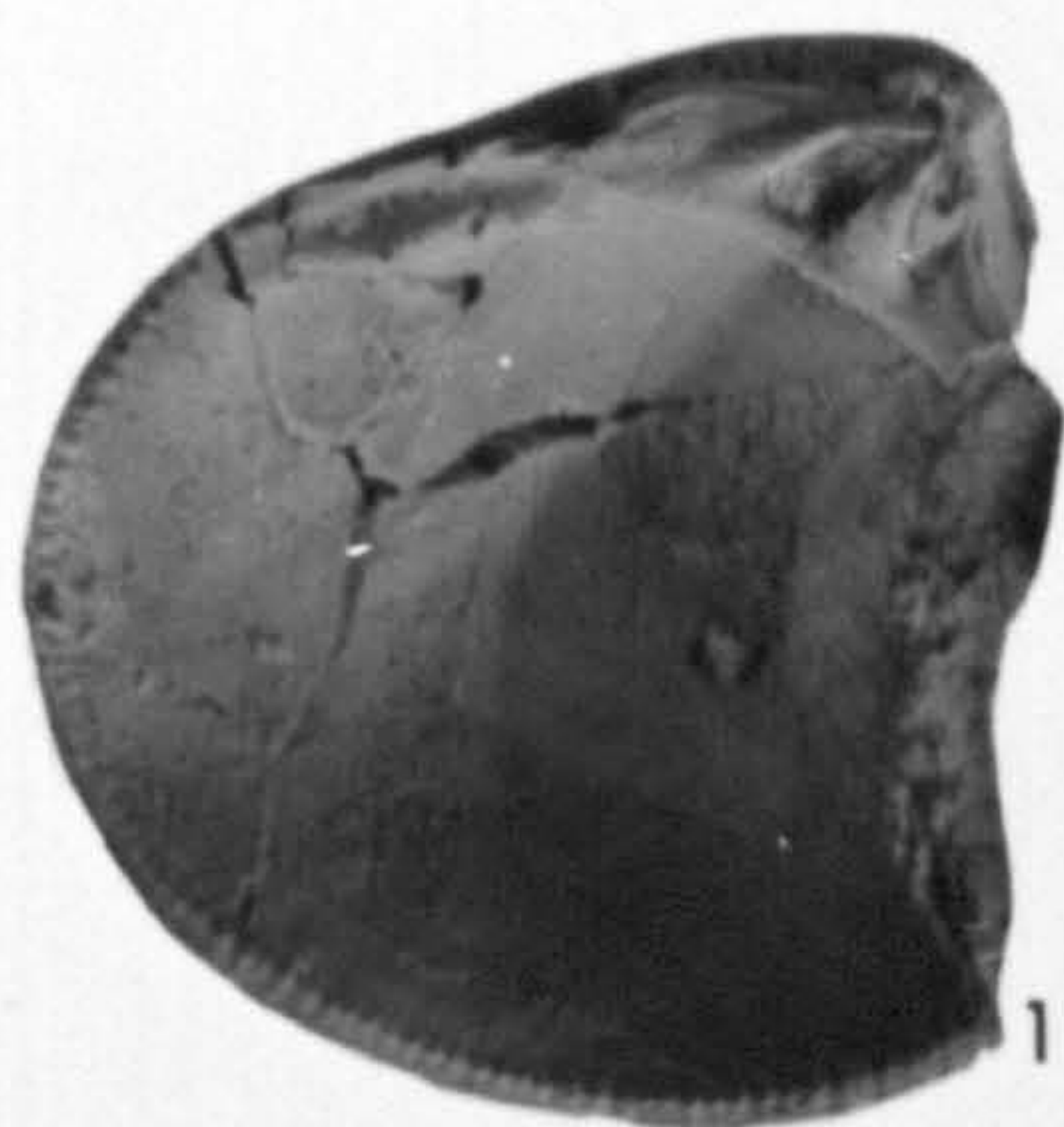
Figs. 21a-c. Neocrassina (Lyapinella) asiatica (Zakharov). SMC. B.11941, steinkern, Spilsby Sandstone unhorizoned, probably Lower Spilsby Sandstone, Claxby, Lincs.



EXPLANATION OF PLATE 19

Figs. 1-7, 7a, b, 8, 9, 10a-f. Neocrassina (Lyapinella) asiatica (Zakharov). 1, SRAK IG.1671, left valve interior; 3, IG.1672, silicone rubber cast of right exterior; 5, IG.1869, silicone rubber cast of right valve exterior, Bed 6 calcareous concretions, Lower Spilsby Sandstone, S. lamplughii Zone, Upper Volgian, Nettleton, Lincs. 2, IG.2336, silicone rubber cast of right valve exterior; 4, IG.2344, silicone rubber cast of right valve exterior; 7a, b, IG.2359, silicone rubber cast of right valve exterior; 9, IG.2351, silicone rubber cast of right valve; 10a-f, silicone rubber casts of left and right valves, Bed 1 calcareous concretions, Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, High Barn, West Keal, Lincs. 8, IGS CE 3469, silicone rubber cast of right valve interior, erratic block of Lower Spilsby Sandstone, ?P. oppressus Zone, Middle Volgian, Leziate, Norfolk.

Figs 6a-c. Neocrassina (Lyapinella) aff. asiatica (Zakharov). SRAK IG. 2137, silicone rubber cast of left valve exterior, Bed 2, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.

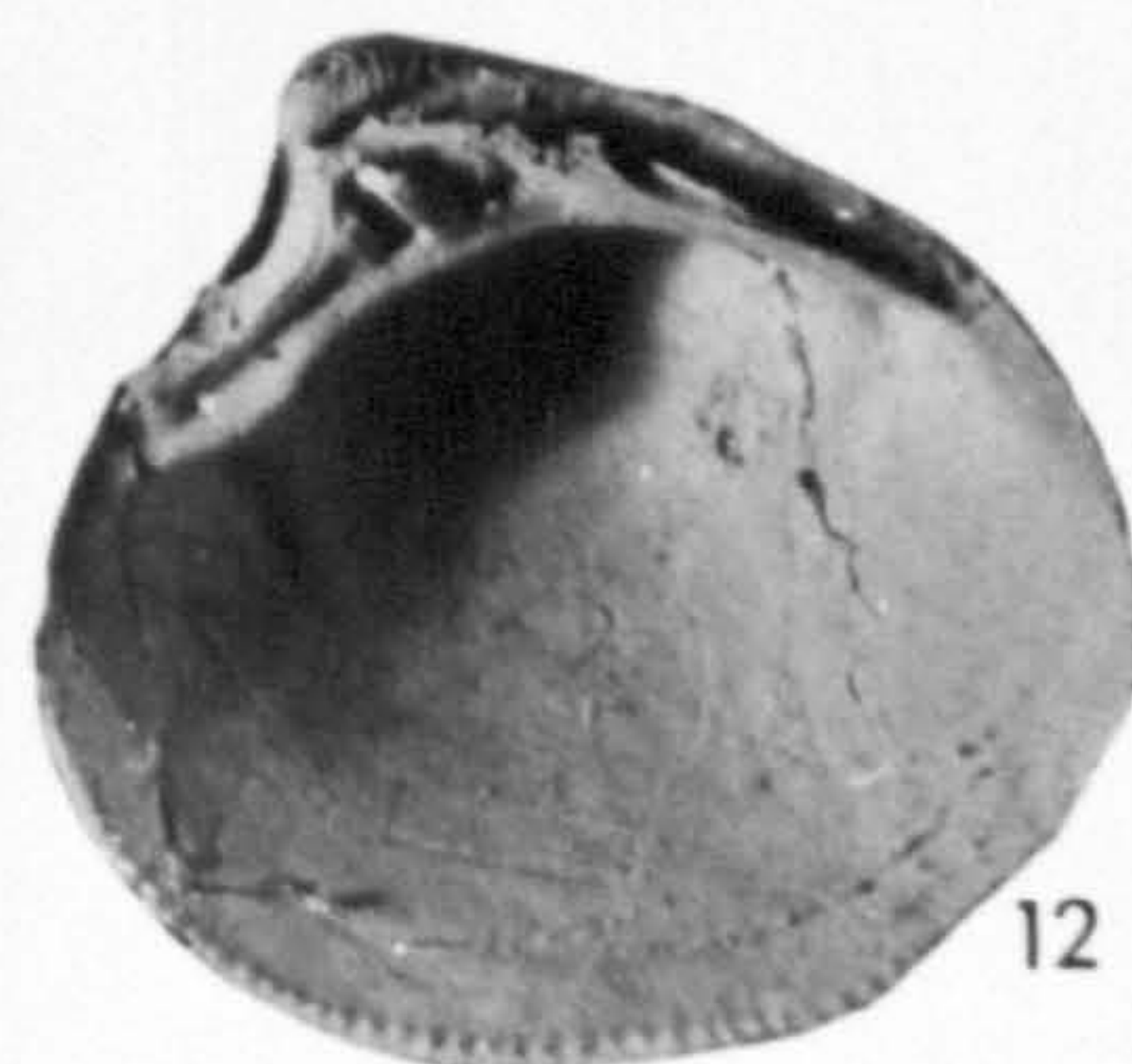
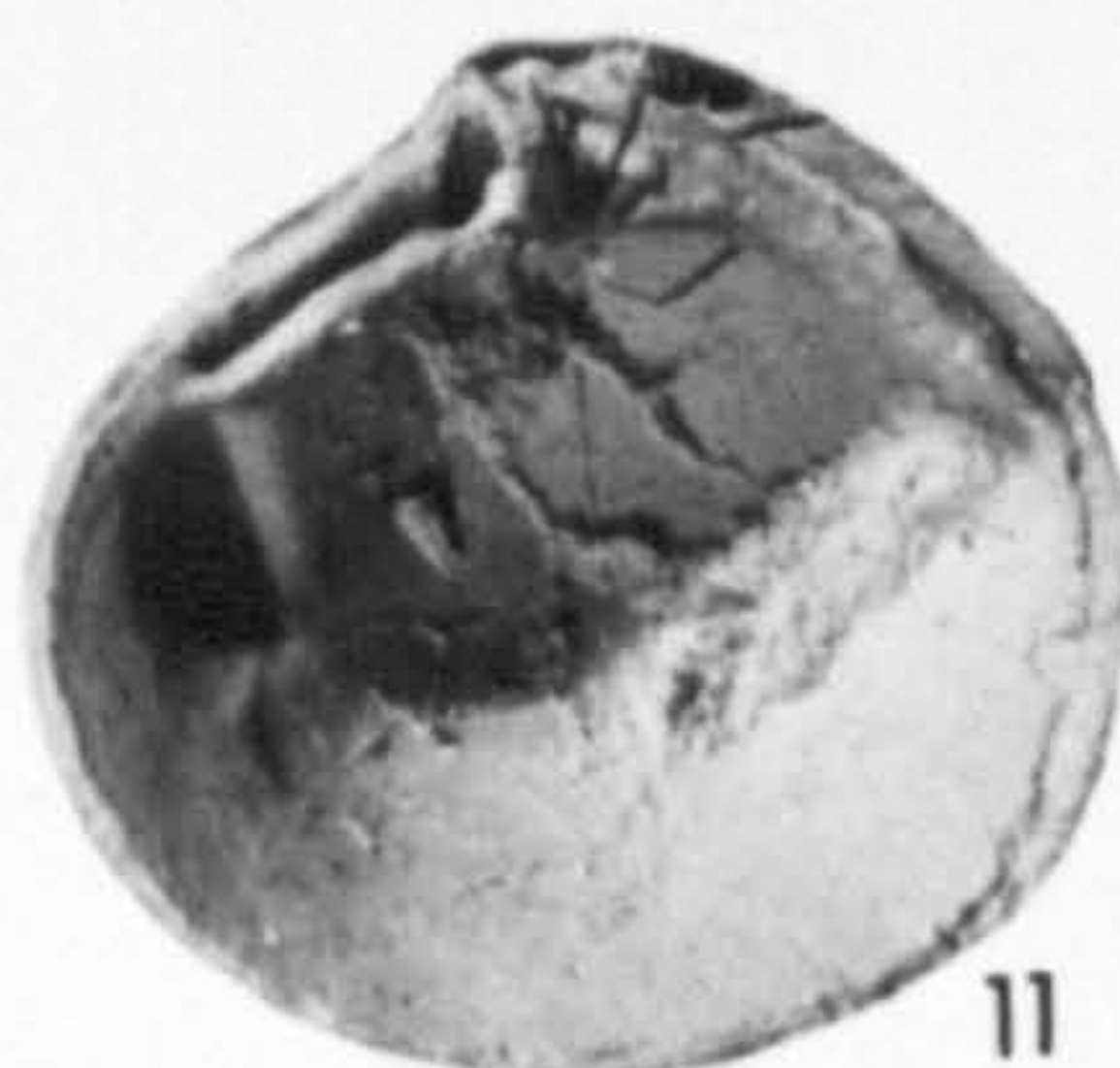
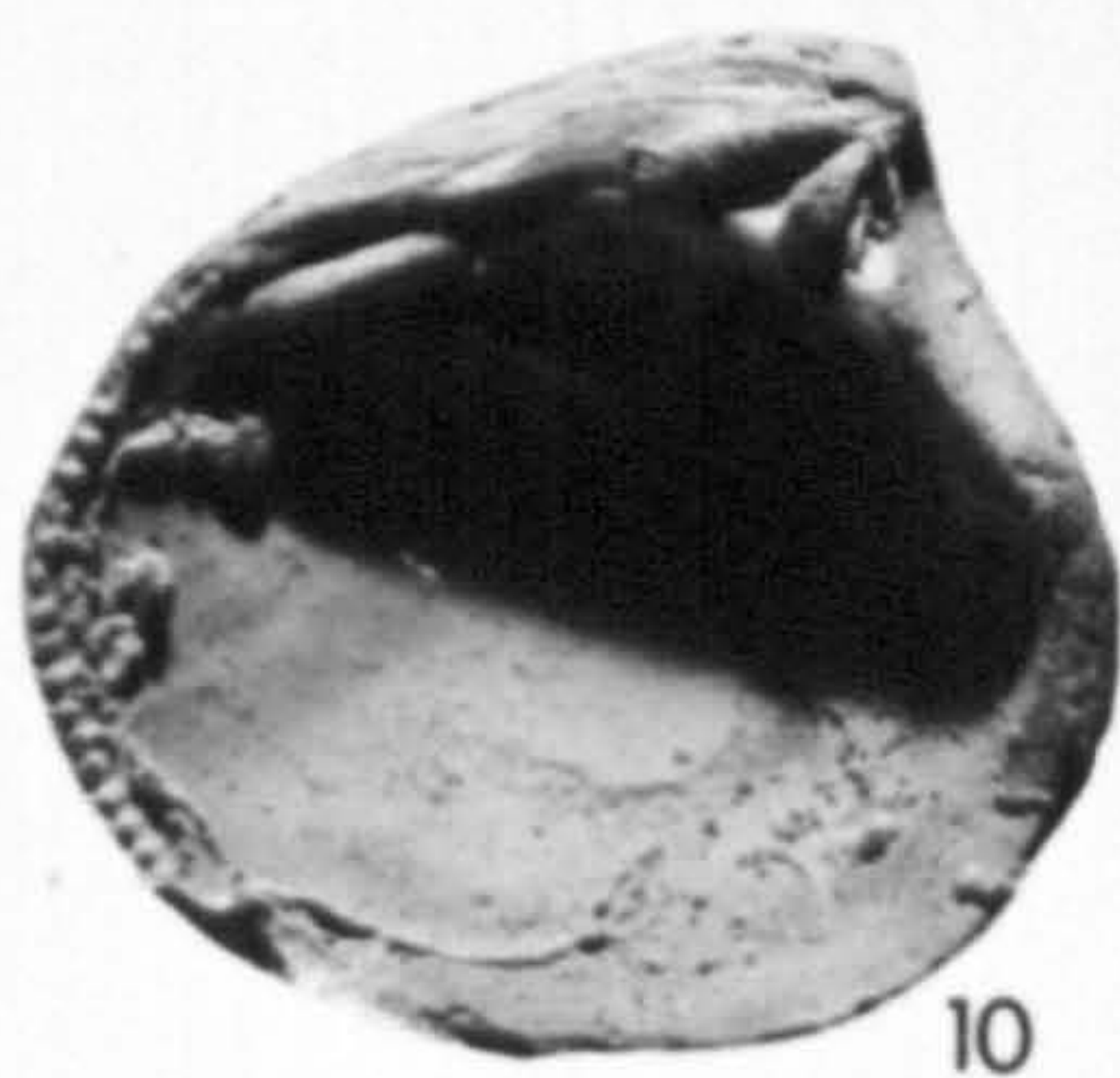
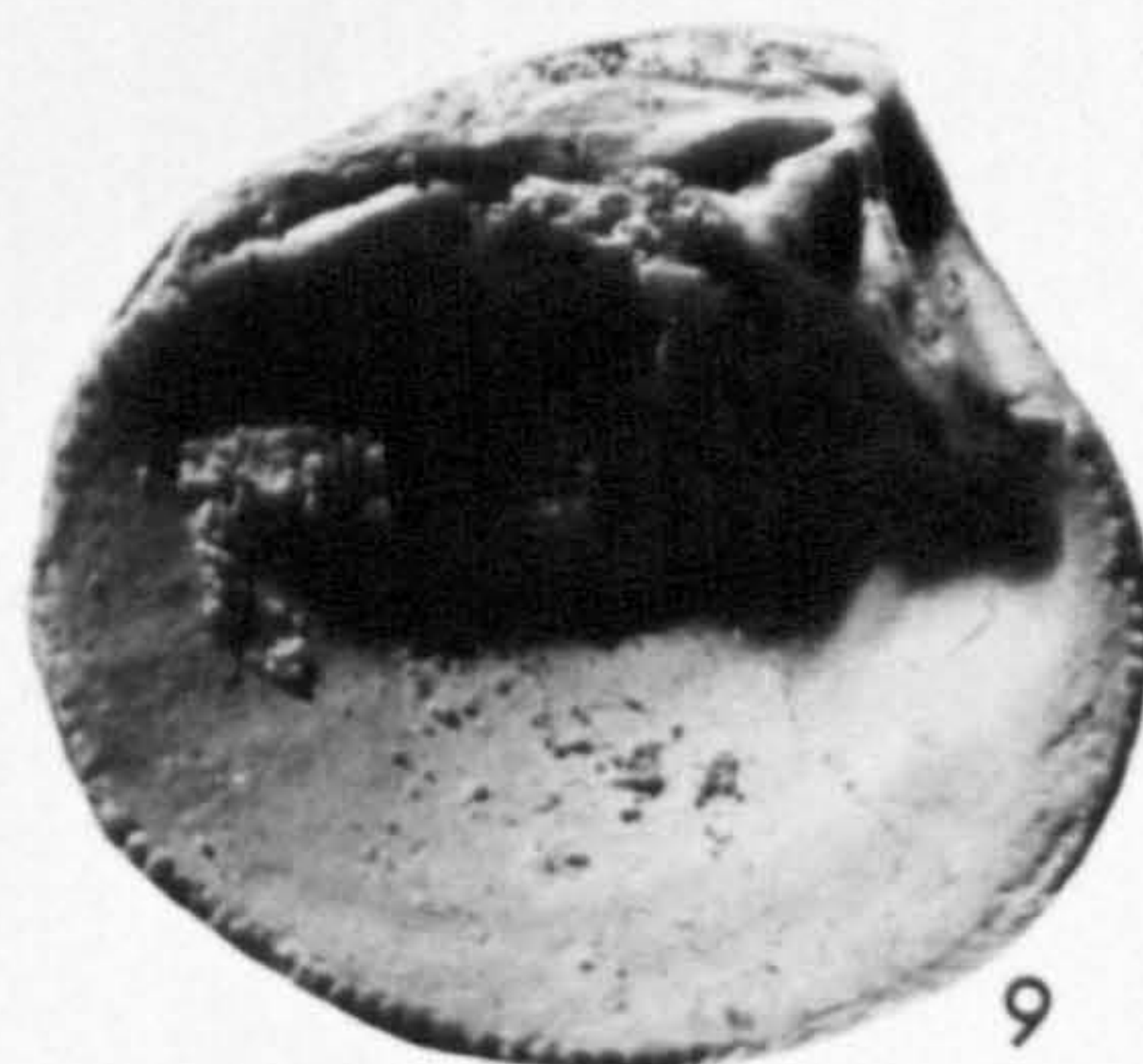
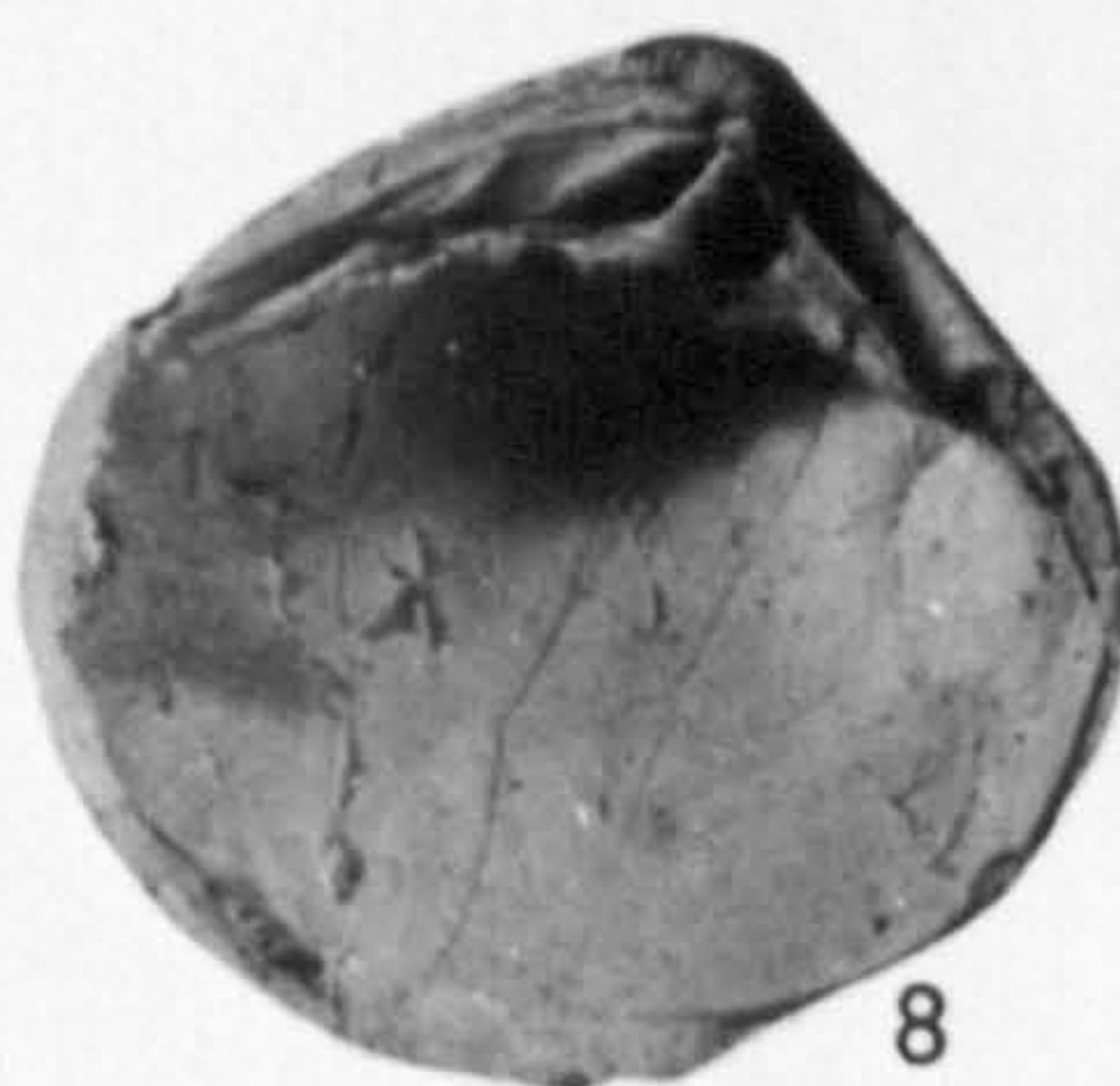
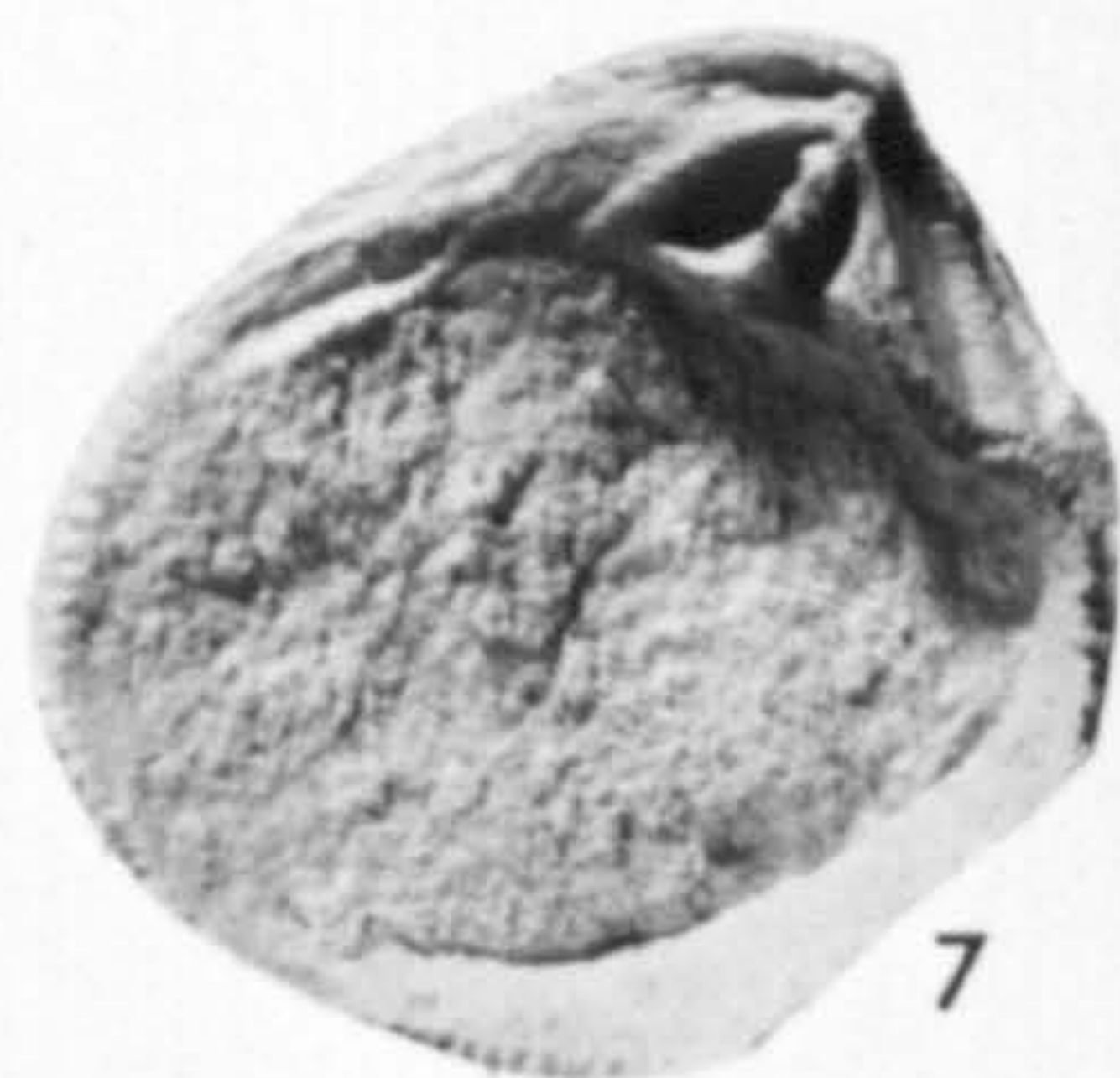
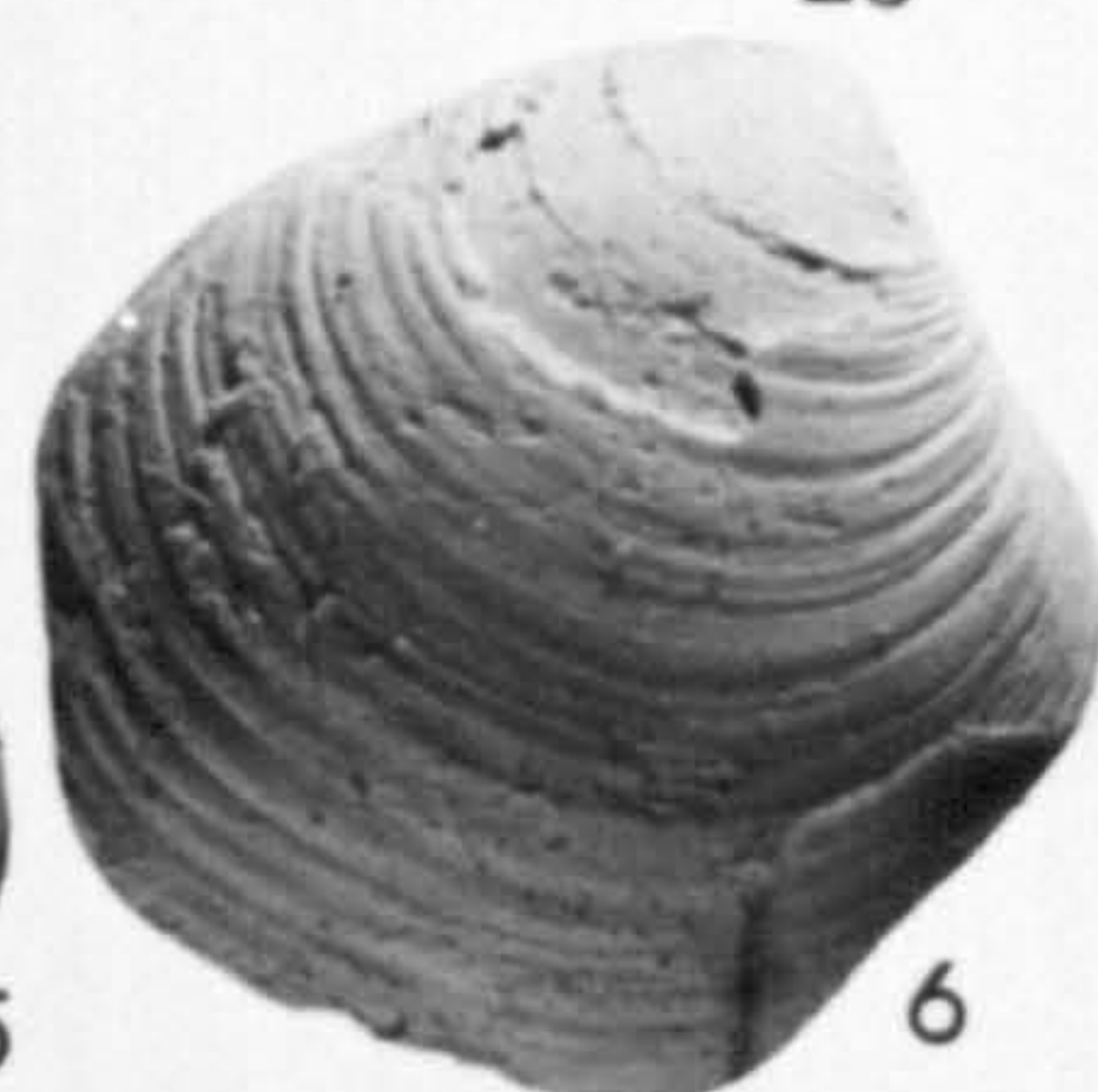
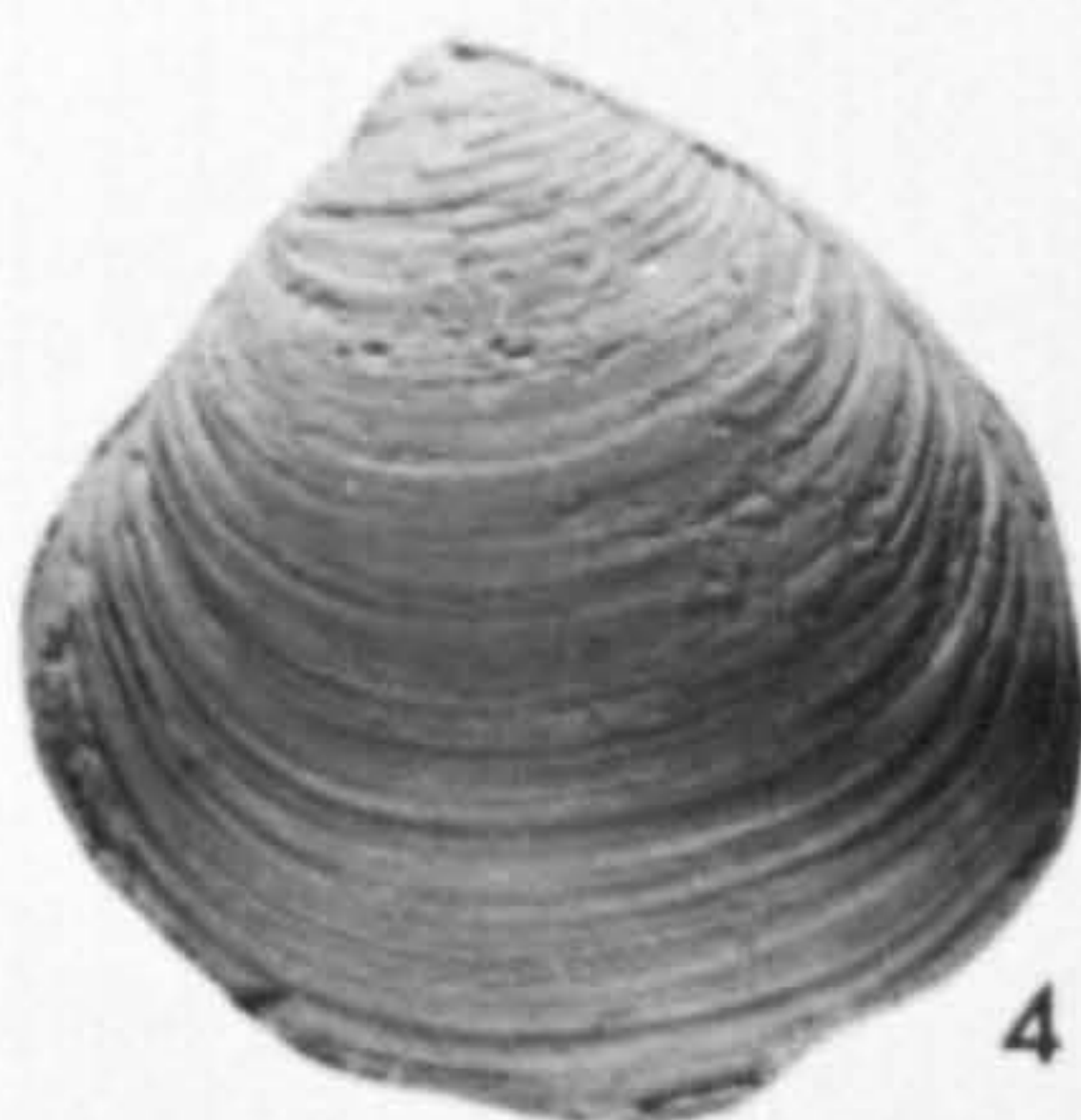


EXPLANATION OF PLATE 20

Figs. 1a, b, 2a-c, 3-12. Paratypes of Neocrassina (Lyapinella) greenlandica sp. nov. 1a, b, ICS CE 3041, silicone rubber cast left lateral and dorsal aspects; 2a-c, CE 2488, silicone rubber cast of right valve exterior; 3, CE 1554, silicone rubber cast of right valve exterior; 4, CE 1554, silicone rubber cast of right valve exterior; 5, WA 3155, silicone rubber cast of right valve exterior; 6, CE 3033, silicone rubber cast of right valve exterior; 7, CE 2453, silicone rubber cast of left valve interior; 9, CE 1591, silicone rubber cast of right valve interior; 10, CE 1588, silicone rubber cast of left valve interior; 11, CE 1566, silicone rubber cast of right valve interior, Mintlyn Beds, H. kochi Zone Ryazanian, West Dereham Flood Relief Channel, Norfolk. 8, CE 4504 silicone rubber cast of right valve interior; 12, CE 4420, silicone rubber cast of right valve interior, Bed 10, Mintlyn Beds, S. stenomphalus Zone, Ryazanian, Mintlyn Wood, Norfolk.

Figs 13a-c. Neocrassina (Lyapinella) duboisiana (d'Orbigny). BMNH L.14438, complete individual in glauconitic sandstone, Middle Volgian?, Tatarovo near Moscow.

PLATE 20



EXPLANATION OF PLATE 21

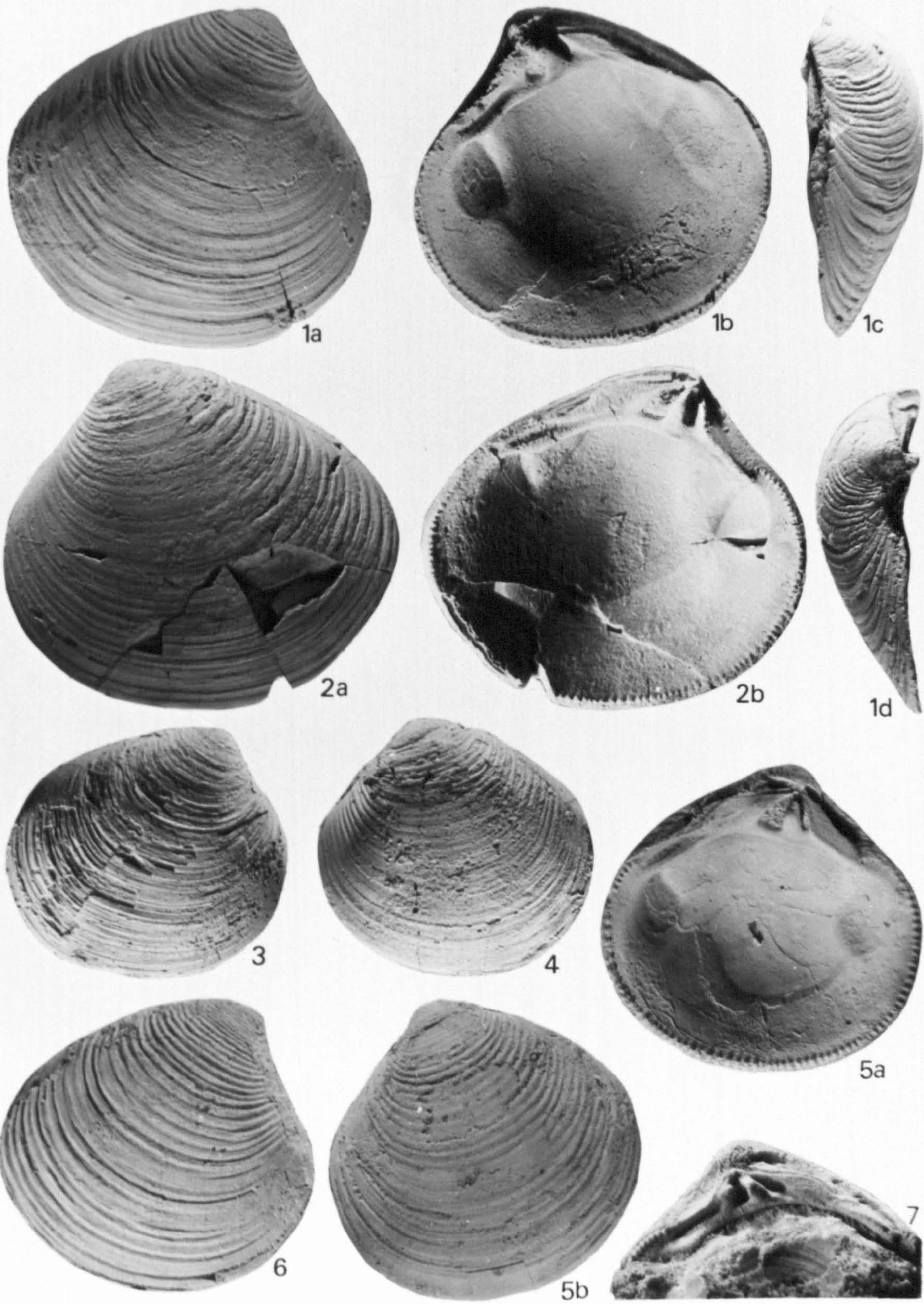
Figs. 1a-d, 2a- b, 3, 4. Neocrassina (Lyapinella) groenlandica sp. nov.

1a-d, paratype, JG.1192, right valve; 2a, b, holotype, JG.1191, left valve; 3, paratype, JG.1194; 4, paratype, JG.1193, left valve, Basal conglomerate, Muslingeelv Member, Hesteelv Formation, H. kochi Zone, Ryazanian, 3 km south of Crinoidbjerg, South Jamesonland, East Greenland, (locality 308 of Spath, 1947).

Figs. 5a, b, 6, 7. Neocrassina (Lyapinella) saemanni (de Loriol),

5a, b, SMC J.16199, left valve showing distinctive weak pallial sinus; 6, J.16197, right valve; 7, J.16177, right valve detail of hinge, Keeping Collection, Shotover Grit Sand, P. pectinatus Zone, Lower Volgian, Swindon, Wilts.

PLATE 21



EXPLANATION OF PLATE 22

Figs. 1a-c, 2a-c. Neocrassina (Pressastarte) weldsi sp. nov. 1a-c, holotype, SRAK IG.2348, silicone rubber cast of left valve; 2a-c, paratype, IG.1561, silicone rubber cast of right valve, Bed 1 concretions, Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, High Barn, West Keal, Lincs.

Figs. 3a-c, 4a-c, 5, 6, 7. Neocrassina (Pressastarte) pelons (d'Orbigny). 3a-c, SRAK IG.2177, silicone rubber cast of left valve; 4a-c, IG.1561, silicone rubber cast of right valve; 5, IG.2169, silicone rubber cast of left valve exterior; 6, IG.2183, silicone rubber cast of left valve interior; 7, IG.3442, silicone rubber cast of right valve interior, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.

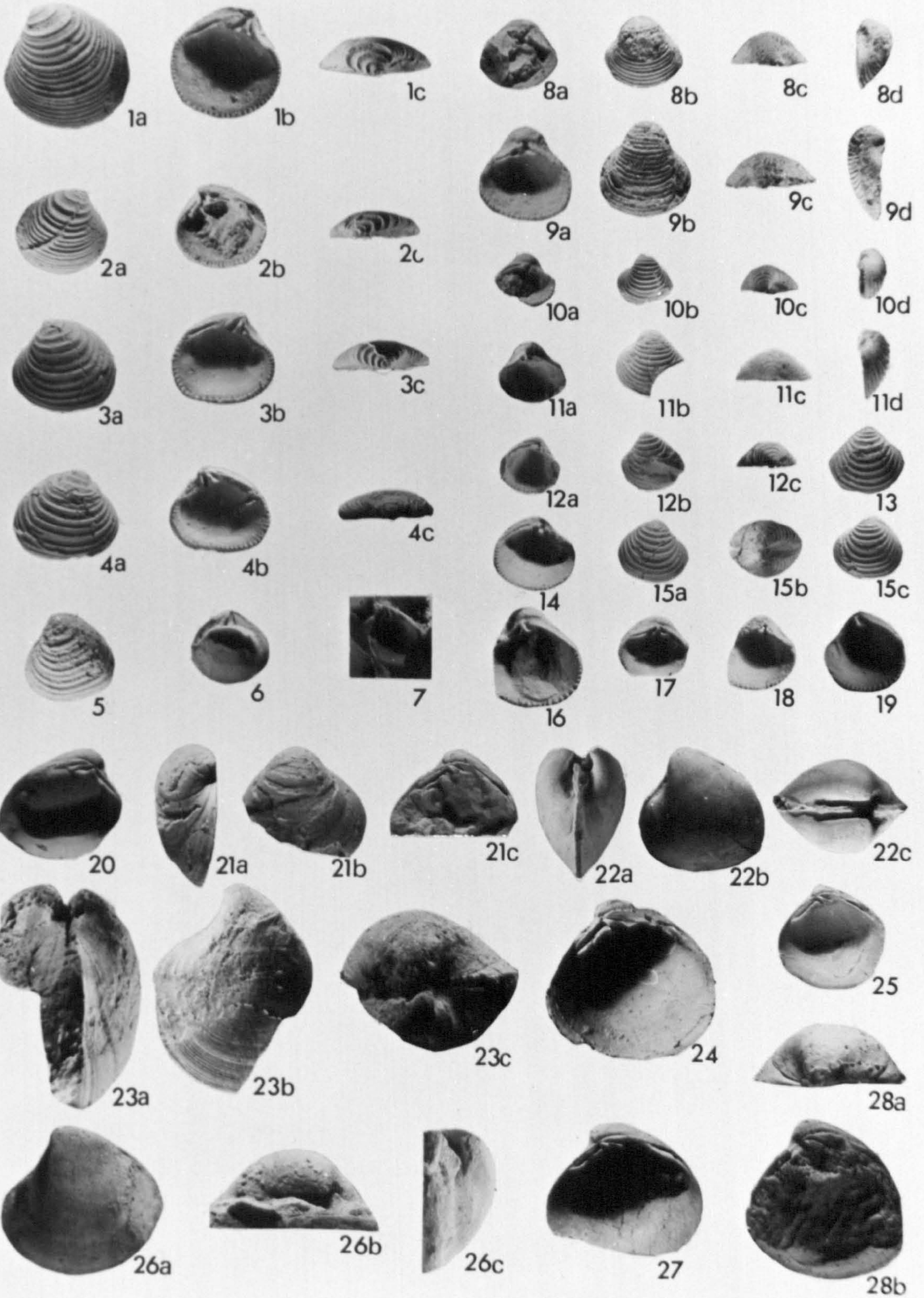
Figs 8a-d, 9a-d, 10a-d, 11a only. Nicaniella (Trautscholdia) claxbiensis (Woods). 8a-d, IG.2347, silicone rubber cast of left valve; 9a-d, IG.2346, silicone rubber cast of right valve, Bed 1 concretions, Lower Spilsby Sandstone, S. preplicomphalus Zone, Upper Volgian, High Barn, West Keal, Lincs. 10a-d, syntype, SMC B.11354, left valve, figured Woods, 1906, pl. 14, fig. 25, Spilsby Sandstone, unhorizoned, Spilsby, Lincs. 11a, IG.3439, silicone rubber cast of right valve interior, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.

Figs 11b-d, 12a-c, 13, 14, 15a-c, 16-19. Nicaniella (Nicaniella) mnevnikensis (Milaschewitsch). 11b-d, SRAK IG.3438, silicone rubber cast of left valve; 12a-c, IG.3444, silicone rubber cast of left valve; 13, IG.3440, silicone rubber cast of right valve; 14, IG.2186, silicone rubber cast of left valve interior; 15a-c, IG.2178, silicone rubber cast of complete individual; 16, IG.3434, silicone rubber cast of right valve interior; 17, IG.2175, silicone rubber cast of right valve interior; 18, IG.1550, silicone rubber cast of left valve interior; 19, IG.3162, silicone rubber cast of right valve interior, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.

Figs. 20, 21a-c, 22a-c, 23a-c, 24, 25, 28a, b. Anisocardia (Antiquicyprina) lincolnshirensis sp. nov. 20, paratype, IG.3228, silicone rubber cast of left valve interior; 21a-c, holotype, IG.2144, silicone rubber cast of right valve; Paratypes: 22, IG.1954, phosphatised steinkern; 24, IG.3249, silicone rubber cast of right valve interior; 25, IG.3216, silicone rubber cast of right valve interior; Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs. 23a,b, IGS CE 2490, silicone rubber cast of paired valves; 28a, b, CE 2505, silicone rubber cast of right valve, Mintlyn Beds, Hectoroceras kochi Zone, Ryazanian, West Dereham Flood Relief Channel, Norfolk.

Figs. 26a-c, 27. Anisocardia (Antiquicyprina) sandringhamensis sp. nov. 26a-c, SRAK IG.581, internal mould of left valve, erratic block of Lower Spilsby Sandstone, P. oppressus Zone, Middle Volgian, Leziate, Norfolk. 27, WA 3283, silicone rubber cast of right valve, Mintlyn Beds, H. kochi Zone, Ryazanian, West Dereham Flood Relief Channel, Norfolk.

PLATE 22



EXPLANATION OF PLATE 23

Figs. 1a, b, 2. Hartwellia (Claxbya) cancriniana (d'Orbigny). 1a, b, SRAK IG.770, internal mould of left valve; erratic block of Lower Spilsby Sandstone, P. oppressus Zone, Middle Volgian, Leziate, Norfolk. 2, IGS WA 3413, silicone rubber cast of right valve interior, Mintlyn Beds, H. kochi Zone, Ryazanian, West Dereham Flood Relief Channel, Norfolk.

Figs 3a-d, 4, 5, 6. Hartwellia (Hartwellia) ryazaniensis sp. nov. 3a-d, holotype, WGS WA 3423, WA 3412, silicone rubber cast of right valve; 4, WA 3159, silicone rubber cast of right valve interior; 5, WA 3307, silicone rubber cast of left valve interior; 6, WA 3416, silicone rubber cast of right valve interior, Mintlyn Beds, H. kochi Zone, Ryazanian, West Dereham Flood Relief Channel, Norfolk.

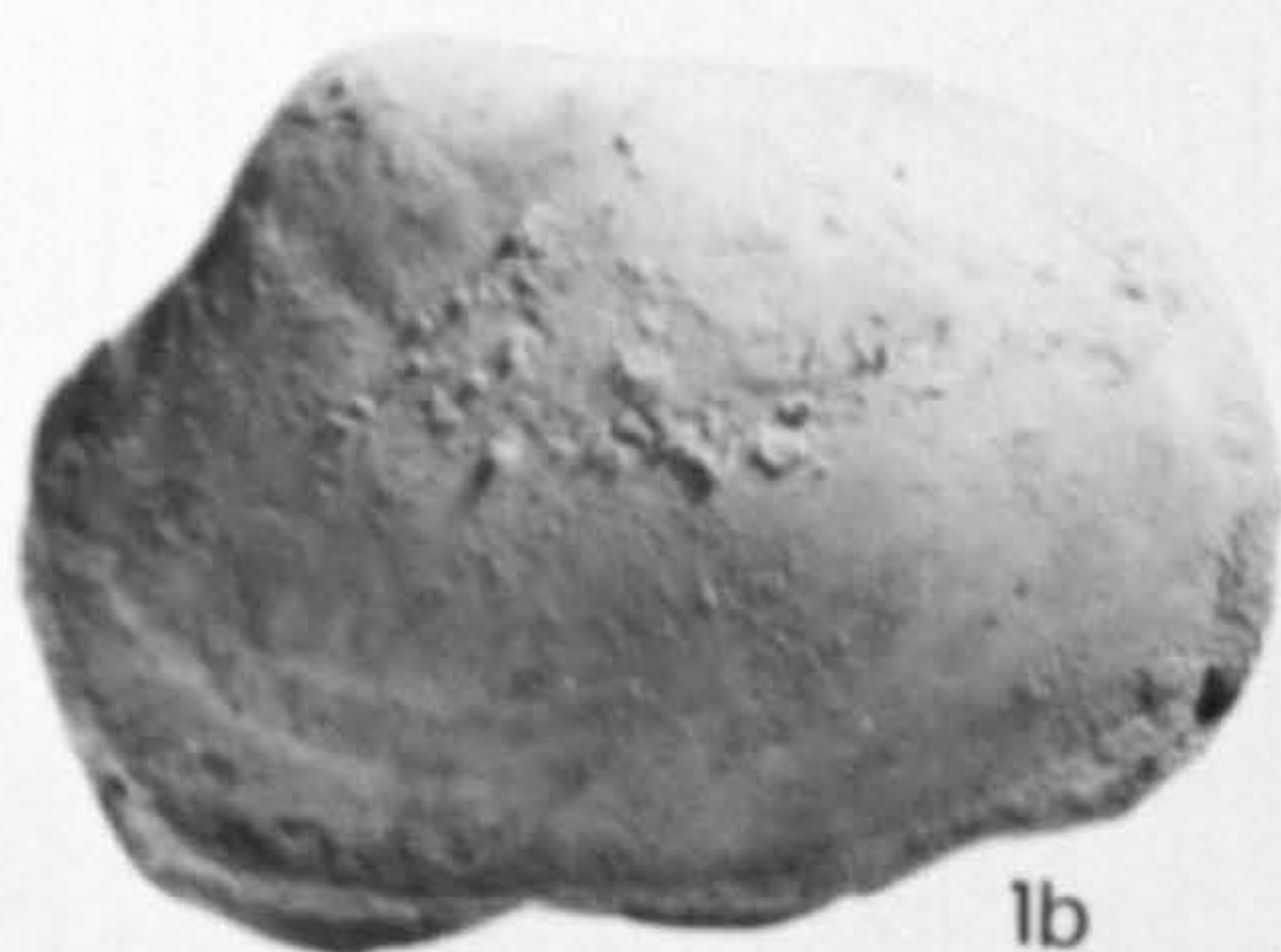
Fig. 7. Corbula sp. CE 4601, silicone rubber cast of several individuals. Bed 10, Mintlyn Beds, S. stenomphalus Zone, Ryazanian, Mintlyn Wood, Norfolk.

Figs 8, 9, Goniomya sp. juv. cf. rawsoni sp. nov. 8, IGS WA 3198, internal mould of left valve; 9, WA 3343, internal mould of right valve, Mintlyn Beds, H. kochi Zone, West Dereham Flood Relief Channel, Norfolk.

Fig. 10. Goniomya rawsoni sp, nov. Holotype, IGS Bb 4411, internal mould of paired valves, slightly crushed, 239½' below surface, top of Bed D (Swinerton 1935) Lower Spilsby Sandstone, S. primitivus Zone, Upper Volgian, Fordington Well, Lincs.



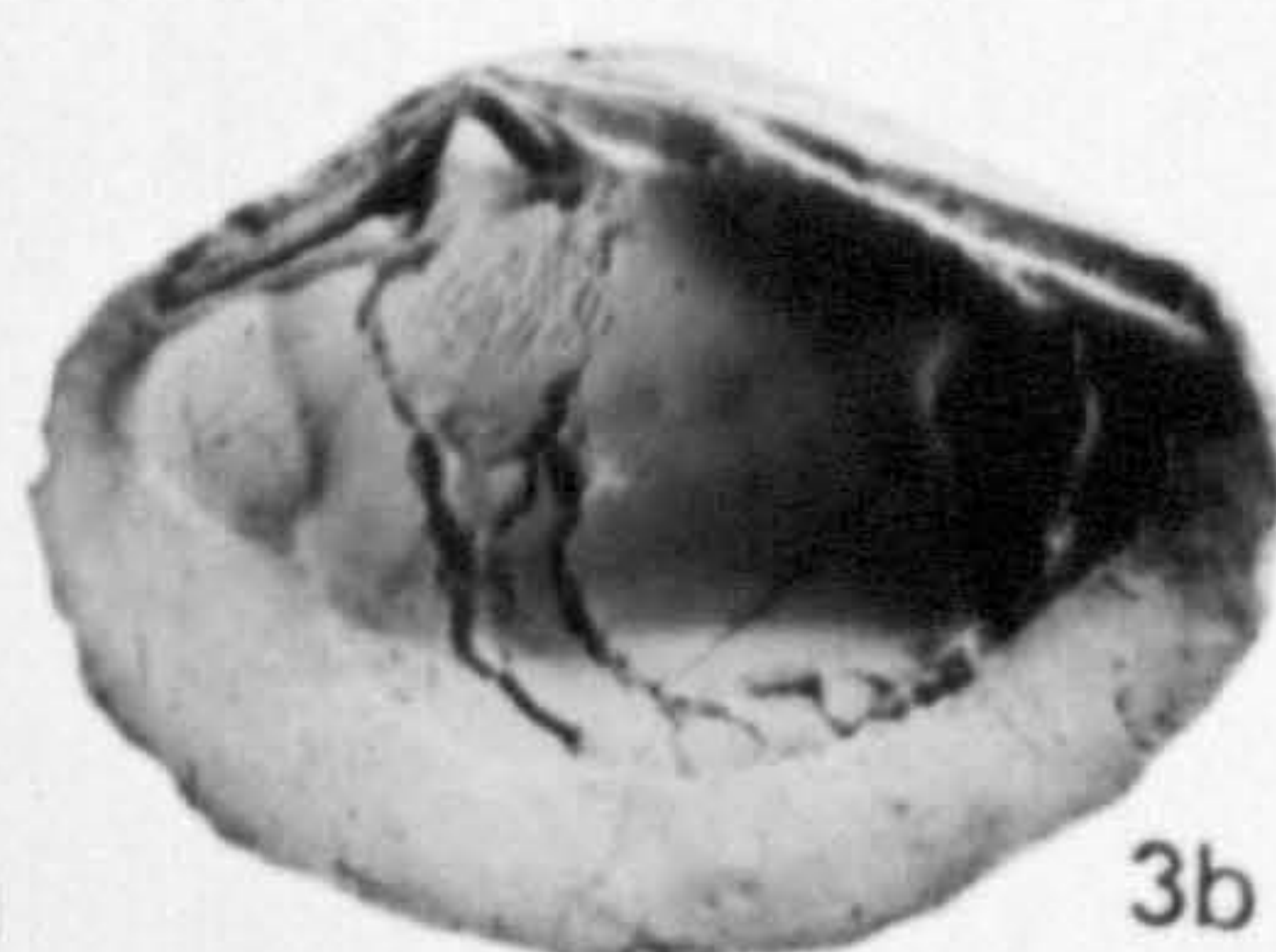
1a



1b



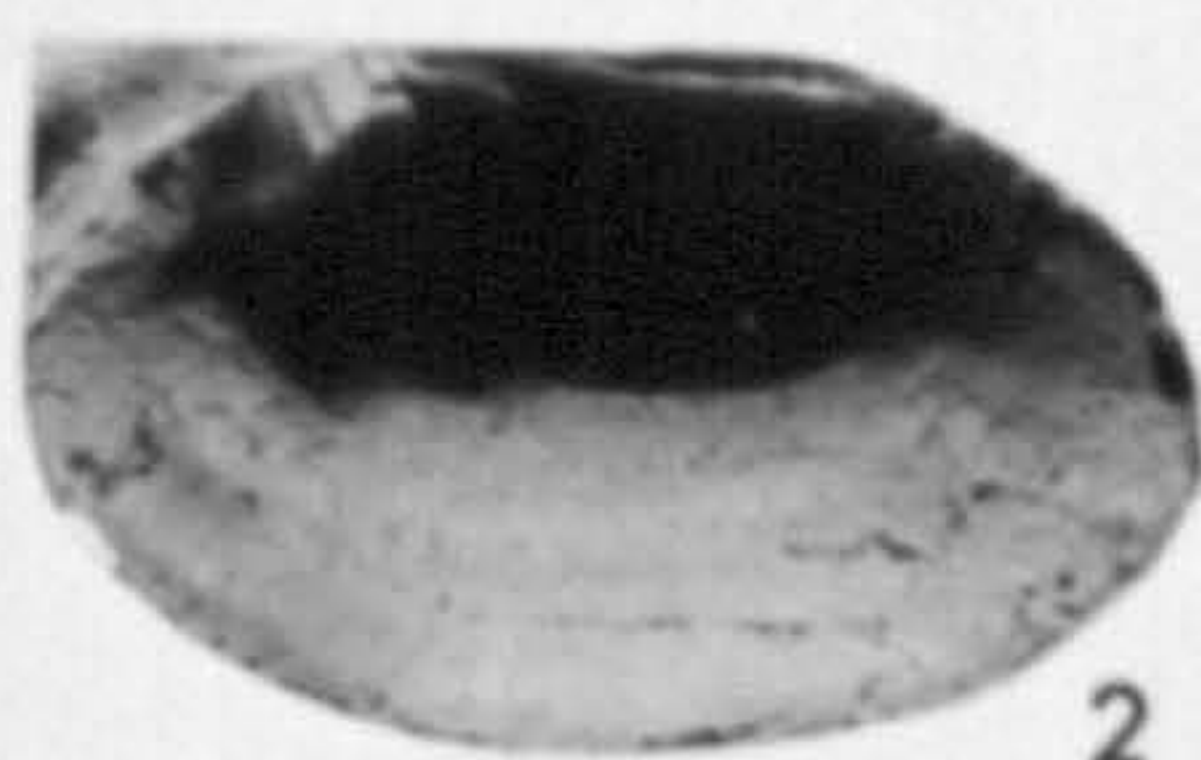
3a



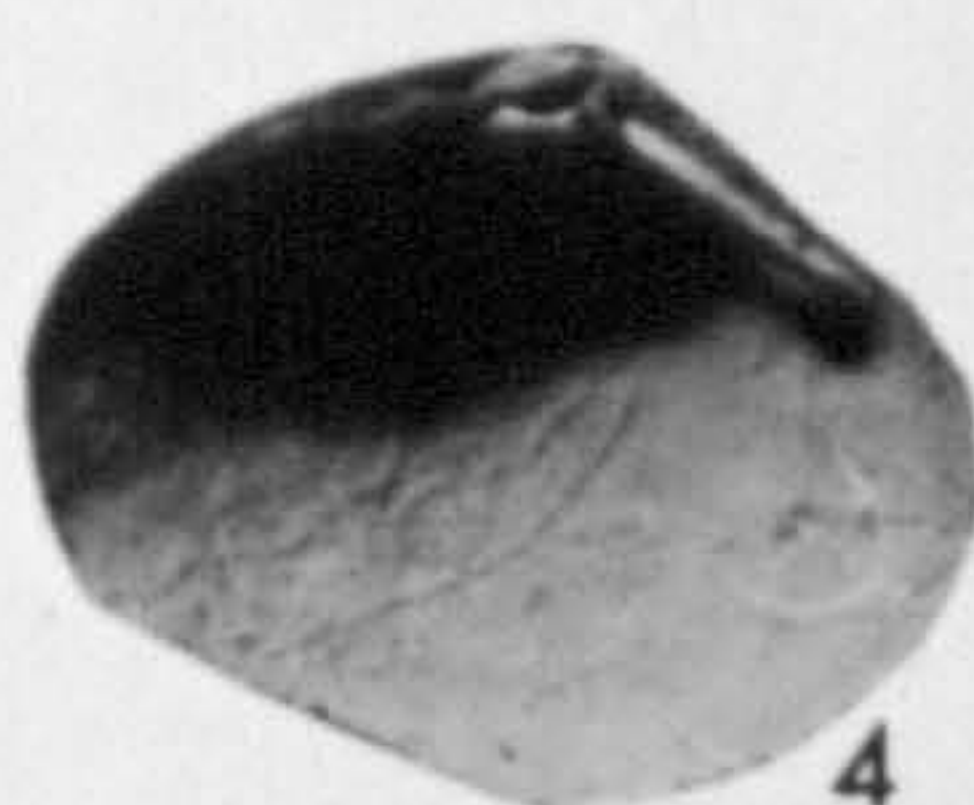
3b



3c



2



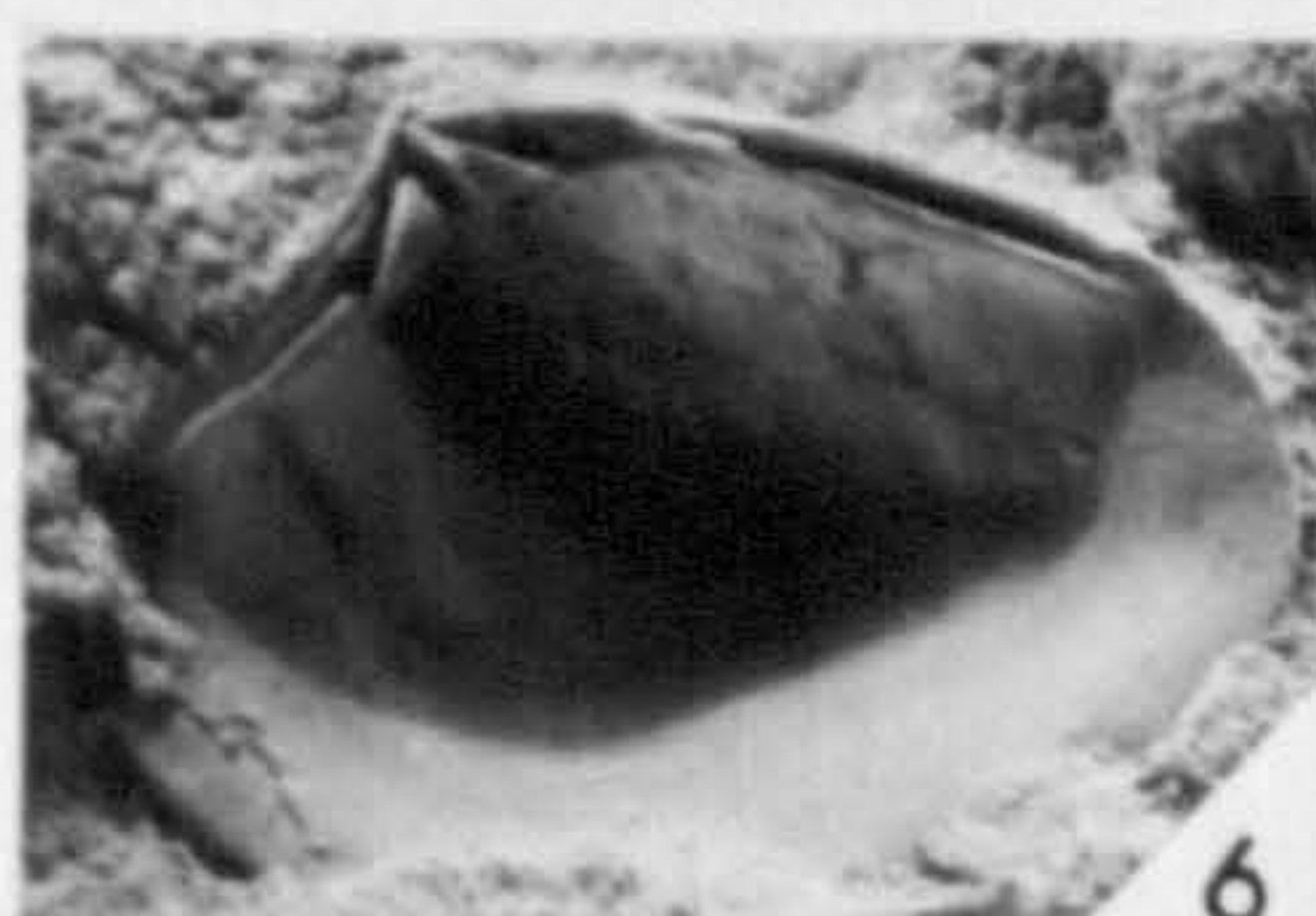
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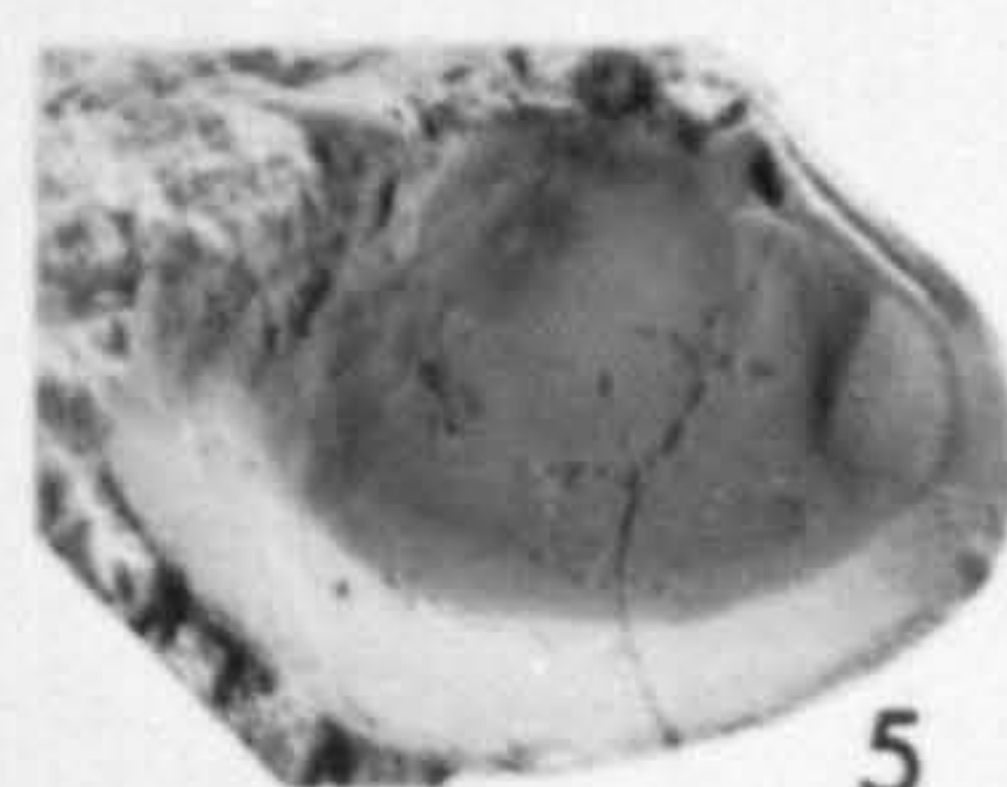
3d



7



6



5



8



9



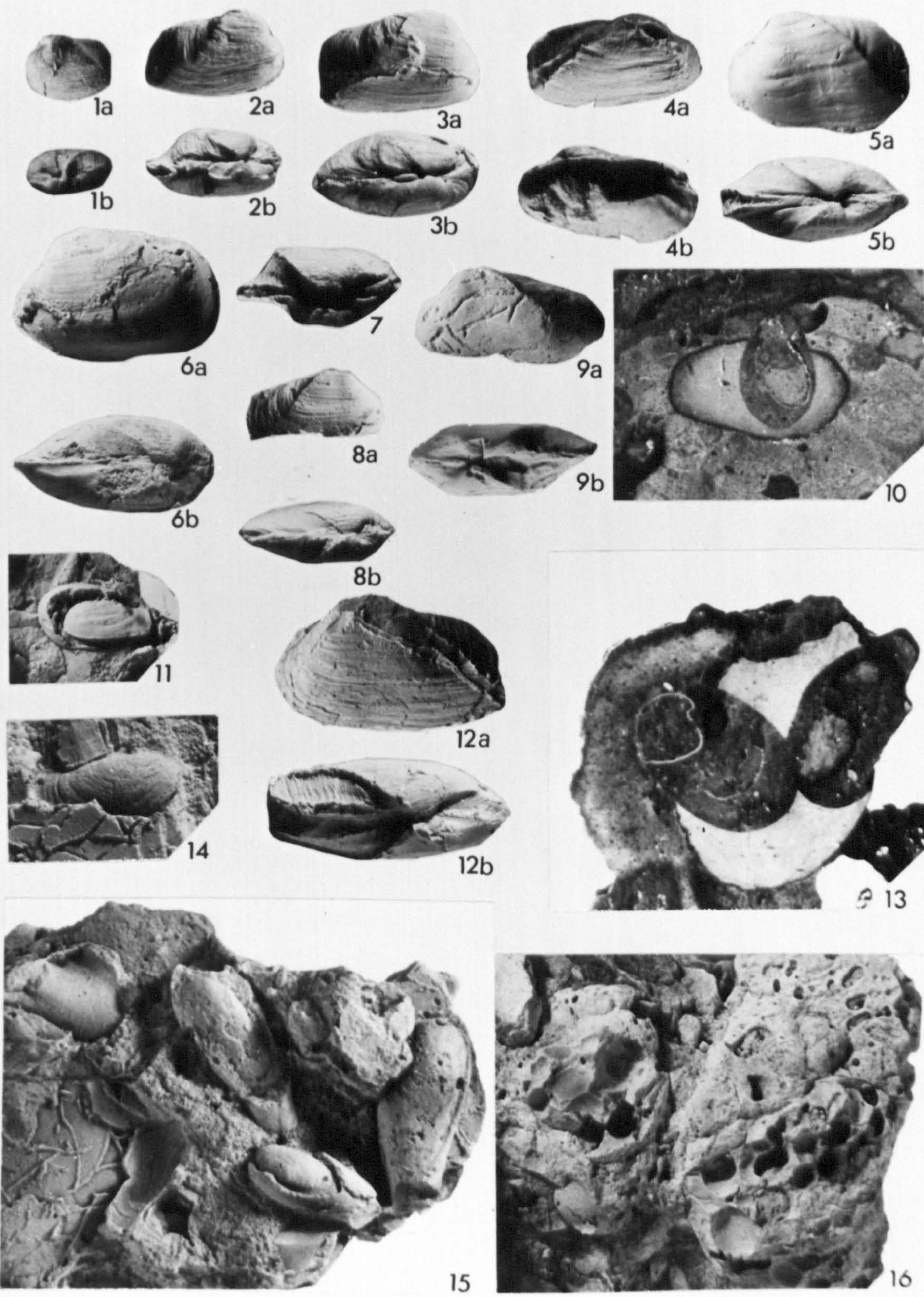
10

EXPLANATION OF PLATE 24

Figs. 1a,b, 2a,b, 3a,b, 4a,b, 5a,b, 6a,b, 7, 8a,b, 9a,b, 10, 11, 12a,b, 13. Hiatella (Pseudosaxicava) foetida (Cox). 1ab, IR.37 silicone rubber cast of complete individual x2; 2a,b, IG.2286, silicone rubber cast of complete individual x2; 3a,b, IG.2291, silicone rubber cast of complete individual x2 (see also plate 25, fig. 8); 4a,b, IG.2288, silicone rubber cast of right valve x2; 5a,b, IG.1112, phosphatised steinkern x2; 6a,b, IG.2298, phosphatised steinkern with some shell adhering x2; 7, IG.1099, silicone rubber cast of left valve exterior x2; 8a,b, IG.2034, silicone rubber cast of complete individual x2; 9, IG.2028, phosphatised steinkern x1; 10, IG.3449, polished section showing shell in boring which cuts across margins of phosphatised clast and matrix x2; 11, IG.2309, shell in association with Gastrochaenolites type boring x2; 12, IG.1617, silicone rubber cast of complete individual x2; 13, IG.3448, boring containing two Hiatella individuals, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.

14, 15. Gastrochaena sp. 14, IG.2123, plasticine cast of right valve (seen as mould in fig. 15) x2; 15, IG.2123, Gastrochaena in life position within Gastrochaenolites type borings x2, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.

16. Gastrochaenolites sp. IR.25, phosphatised nodule with corroded surface and only the base of borings visible x1, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.



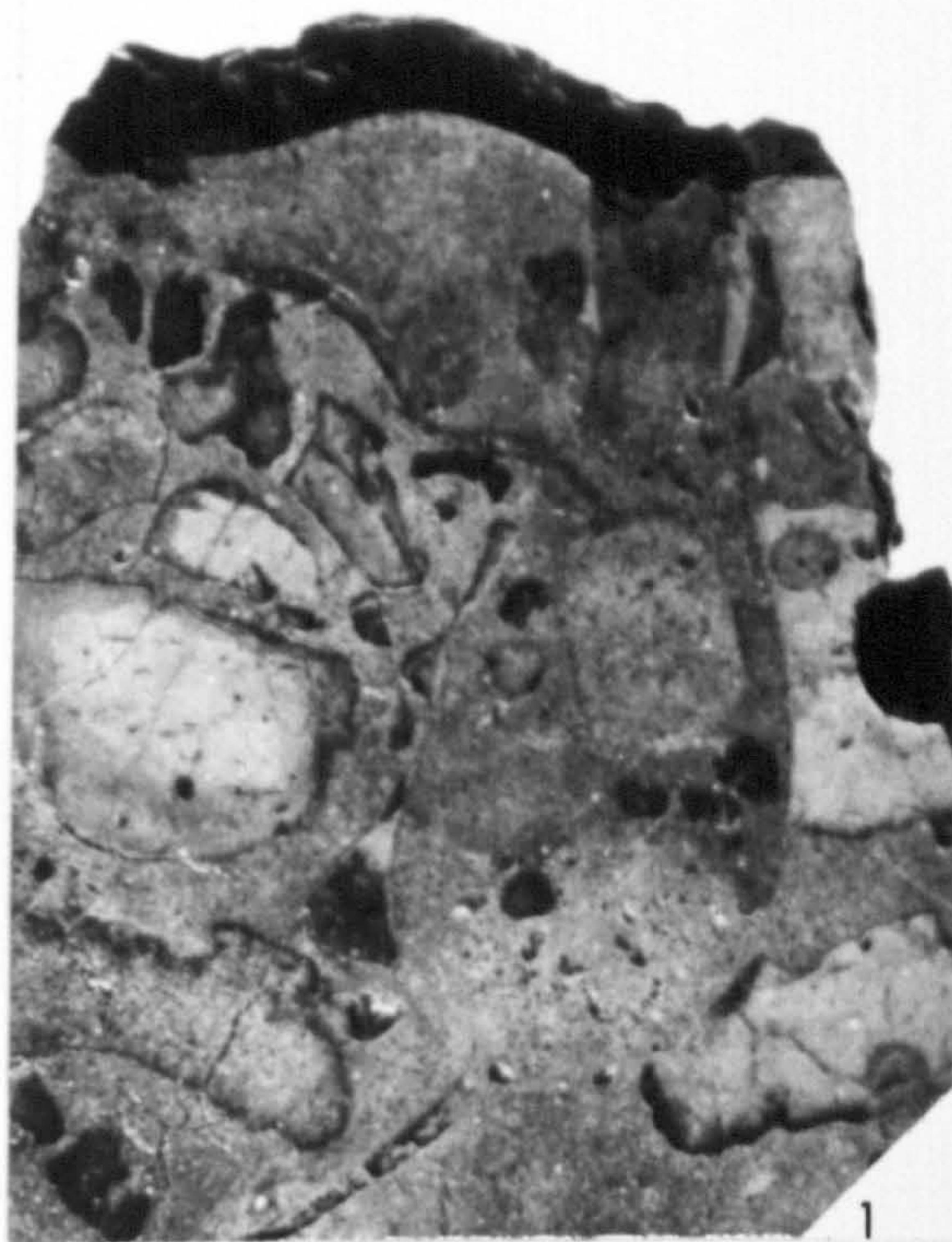
EXPLANATION OF PLATE 25

1a, b, 2-8. Gastrochaenolites sp. 1a,b, IG.1086, 1a, bored bone fragment showing broken open flasks in transverse section with Hiatella in situ, 1b, showing surface of bone with oval openings to flasks x2; 2-8 phosphatised matrix infillings from borings; 2, IR.80, interpenetrating borings x1; 3, IR.49, complete boring x1; 4, IR.51, boring with bent neck x1; 5, IR.87, pair of borings x1; 6, IG.2311, interpenetrating borings x1; 7, IG.2293, boring containing two valves of Hiatella, x2; 8, IG.2291 (see also pl. 24, fig. 3) boring with complete Hiatella (silicone rubber cast) occupying part of the interior, x2, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.

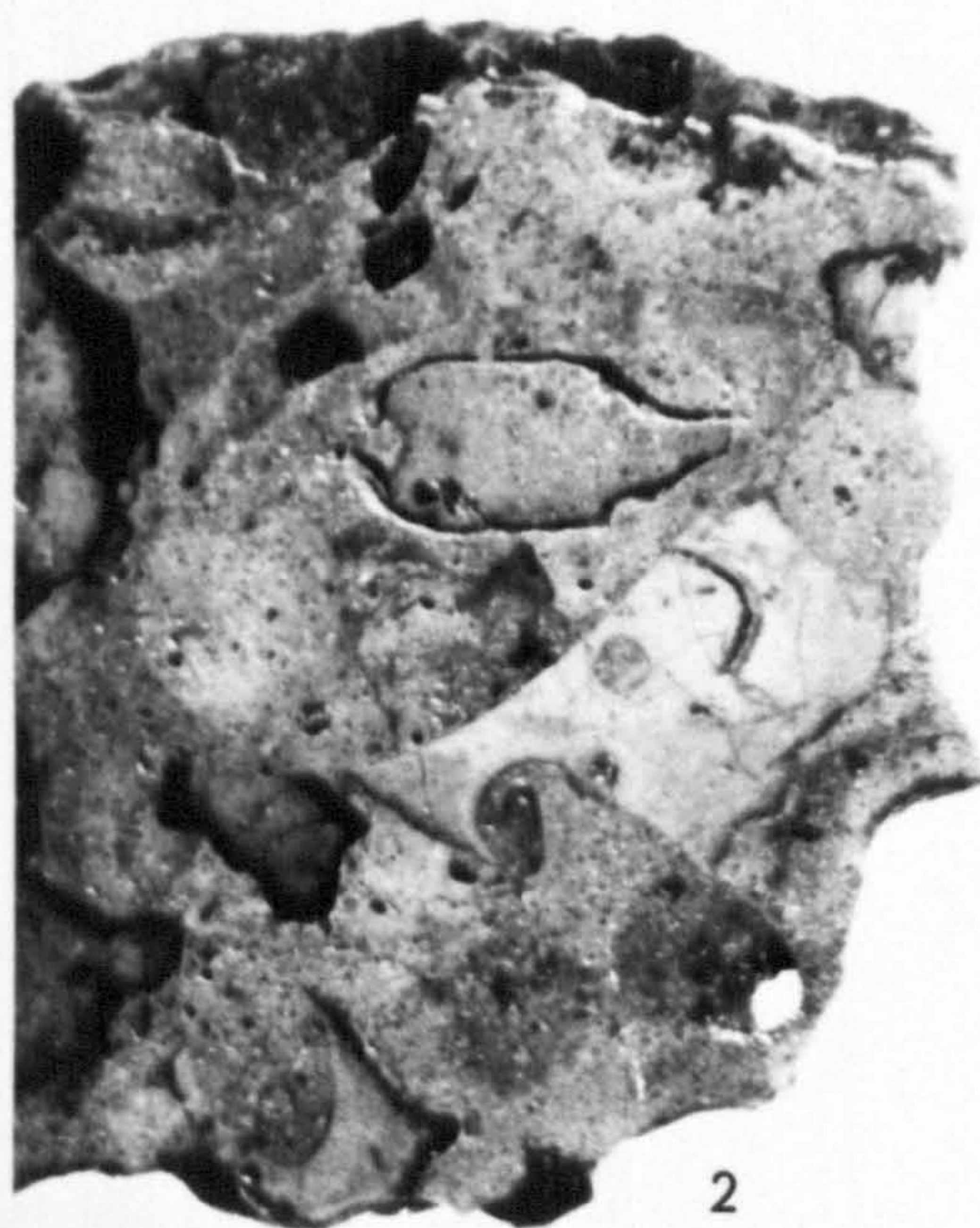


EXPLANATION OF PLATE 26

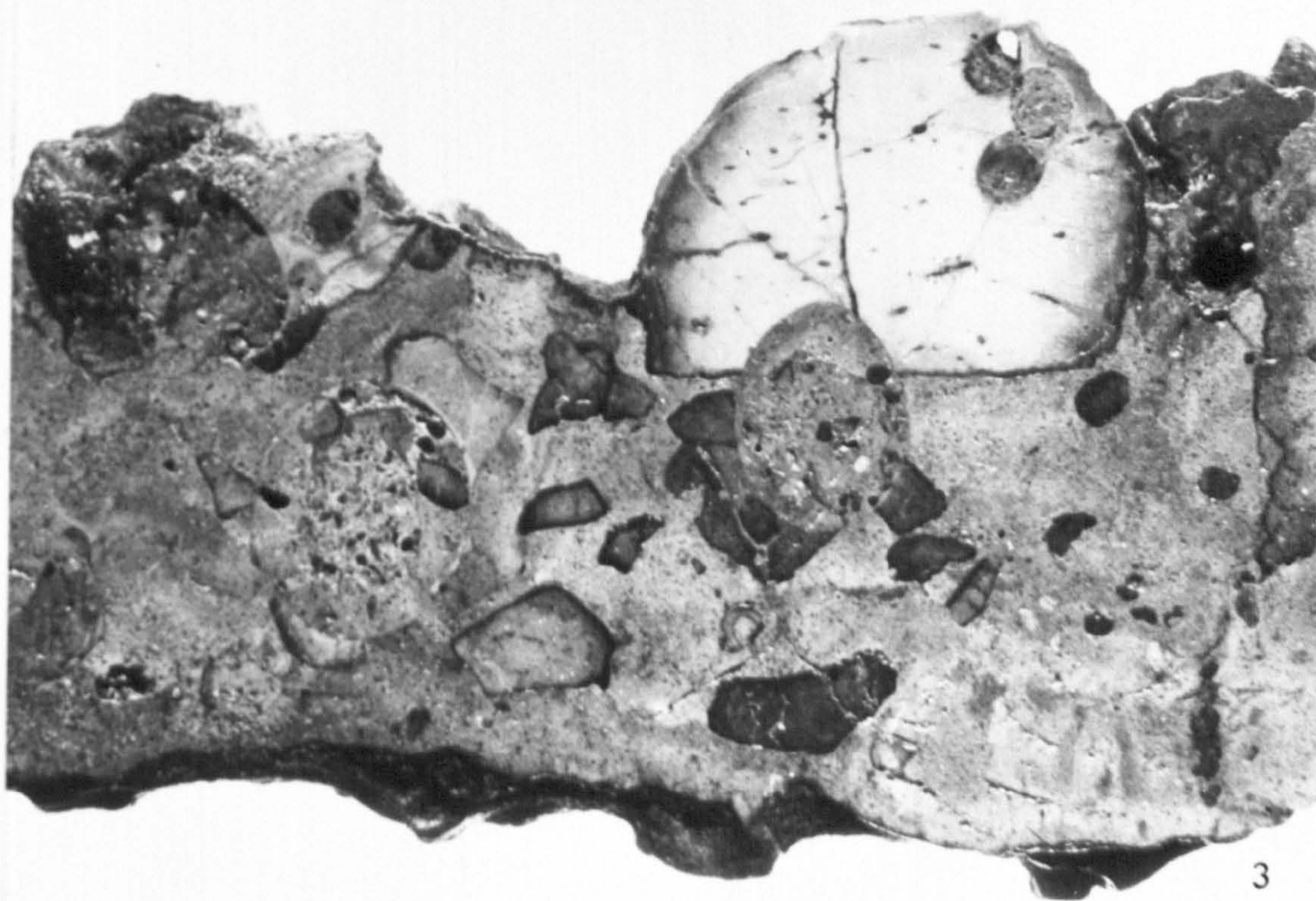
Figs. 1-3, Gastrochaenolites sp. 1, IR.143, boring penetrating evenly phosphatised clasts and matrix, x2; 2, IG.3458, boring containing mould of Hiatella inadequately filling the cavity, x2; 3, IR.140, borings showing circular cross section, x2, Basal Spilsb/ Nodule Bed, Middle Volgian, Nettleton, Lincs.



1



2



3

EXPLANATION OF PLATE 27

Figs. 1a-c, 2, 3a, b, 4. Girardotia compressa (J. de C. Sowerby)

1a-c, neotype, IGS Huddleston Collection, Y1558, composite mould, Kimmeridge Clay, Shotover, Oxfordshire. 2, SRAK IG.2116, phosphatised internal mould of right valve; 3a, b, IG.1386, silicone rubber cast of incomplete pair of valves; 4, IG.3123, silicone rubber cast of left valve exterior, Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincs.

Figs. 5, 6a-c, 7, 8a-c. Girardotia wrighti sp. nov. 5, paratype, IGS CE 4660, silicone rubber cast; 6a-c, paratype, CE 5026, steinkern; Bed 9, Mintlyn Beds, S. stenomphalus Zone, Ryazanian, Mintlyn Wood, Norfolk. 7, holotype, BMNH Wright Collection, 4795, left valve, lower part of the Tealby Clay, Hauterivian, Nettleton, Lincs. 8a-c, paratype, IGS R27/96, Claxby Ironstone, Hundleby Brickyard, Lincs.



